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VOLUME 65
1978

ANNALS
OF THE
MISSOURI BOTANICAL GARDEN

THE HECKMAN BINDERY, INC. N. MANCHESTER, INDIANA

Published by the Missouri Botanical Garden Press, St. Louis, Missouri 63110.
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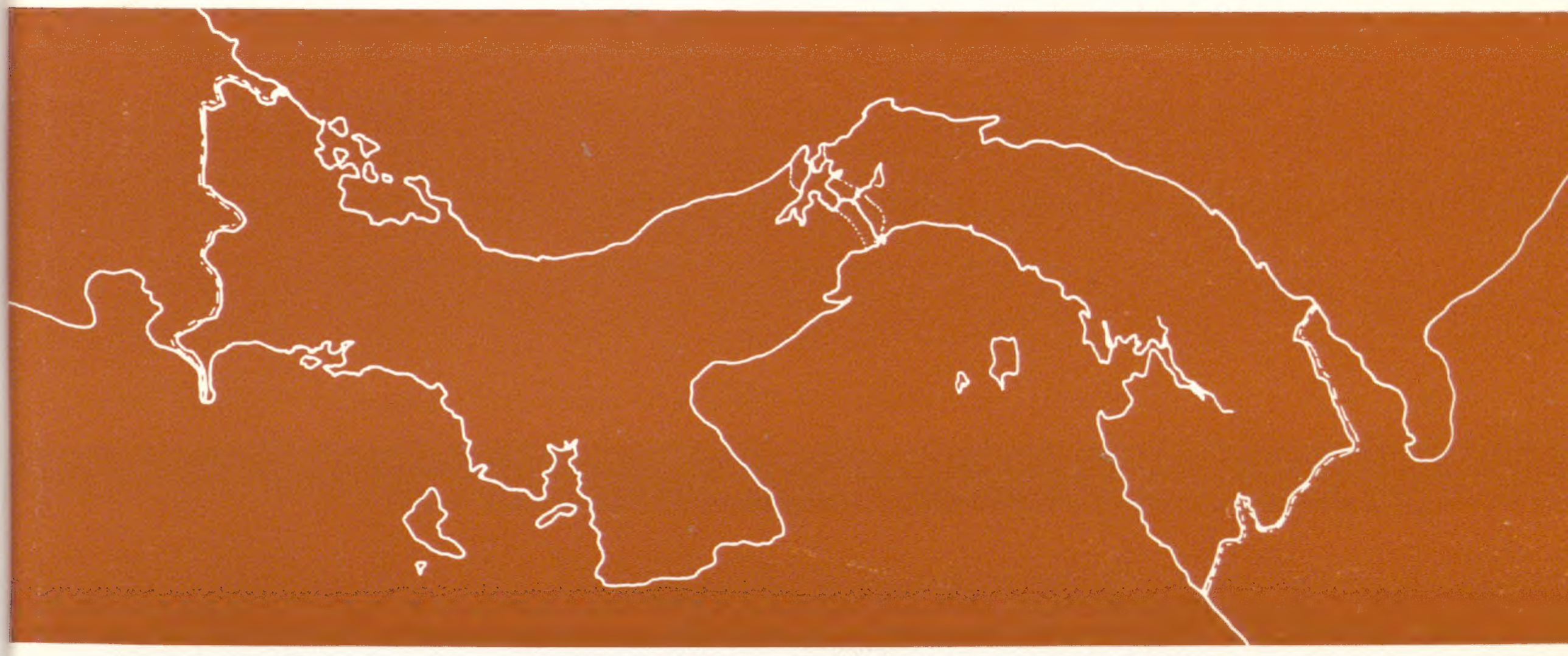

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Published four times a year by the Missouri Botanical Garden Press,
St. Louis, Missouri 63110.

For subscription information contact the Business Office of the Annals,
P.O. Box 368, 1041 New Hampshire, Lawrence, Kansas 66044.

Subscription price is $40 per volume U.S., Canada, and Mexico,
$45 all other countries. Four issues per volume.

Second class postage paid at Lawrence, Kansas 66044

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ANNALS
OF THE
MISSOURI BOTANICAL GARDEN

VOLUME 65 1978 NUMBER 1

FLORA OF PANAMA[1]

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part IV

FAMILY 37. SALICACEAE

W. G. D'ARCY[2]

Trees or *shrubs*, dioiceous or rarely monoecious, glabrous or pubescent; branching alternate. *Leaves* mostly deciduous, alternate, simple, mostly serrate or denticulate, somewhat sclerophyllous, petiolate; stipules deciduous or foliaceous and sometimes persistent; buds covered with one or more deciduous scales. *Inflorescences* in dense erect or lax racemes (aments, catkins), terminal or on short shoots, the rachis mostly with leafy bracts, the pedicels with small, cuculate, entire bracteoles. *Flowers* with the perianth represented by basal glands or a disc; *male flowers* with stamens 2–many, the filaments free or connate, the anthers 2-celled, longitudinally dehiscent; *female flowers* with the ovary sessile or stipitate, sometimes pubescent, 1-locular, the placentas 2–4, parietal, several ovuled, the ovules erect, anatropous, 1(–2)-tegmic, the style solitary or wanting, the stigmas 2–4, often sessile, digitiform. *Fruit* a capsule, dehiscing to the base into 2–4 recurving valves; seeds mostly numerous, often compressed, copiously long-ciliate (comose), the embryo straight, the endosperm nuclear, scant.

The Salicaceae comprises 2 genera, *Salix* and *Populus*, best represented in north temperate regions but also widespread in the tropics; they are absent in Australia, the South Pacific and Southeast Asia. Some species grow north of the Arctic Circle. Both genera have wind-dispersed seeds and many species are well-adapted to wet habitats. *Populus* has wind-pollinated flowers while in *Salix* insects are important in pollination, although reduction of the flowers suggests

[1] Assisted by National Science Foundation Grant DEB 77-04300, W. G. D'Arcy (principal investigator).

[2] Missouri Botanical Garden, 2345 Tower Grove Avenue, St. Louis, Missouri 63110.

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an approach to facultative wind pollination. The family appears to be reduced in floral features from more generalized ancestors. Although a number of possible ancestral relatives have been postulated, no such candidate has received widespread acceptance. The one species of this family known from Panama is also the sole species native in South America. Other species of *Salix* are known in Central America, and species of *Populus* occur in southern Mexico.

Literature:

Schneider, C. 1917. A conspectus of Mexican, West Indian, Central and South American varieties of *Salix*. Bot. Gaz. (Crawfordsville) 65: 1–41.

———. 1919. Notes on American Willows V. The species of the *Pleonandrae* group. J. Arnold Arbor. 1: 1–32.

———. 1921. Notes on American Willows XII. A systematic enumeration of the sections, species, varieties and forms of American Willows. J. Arnold Arbor. 3: 61–125.

1. SALIX

Salix L., Sp. Pl. 1015. 1753; Gen. Pl., ed. 5. 447. 1754. TYPE: *S. alba* L.

Dioecious *shrubs* or *trees*, often slender and flexuous, often from a subterranean caudex; branching alternate. *Leaves* mostly deciduous, alternate, simple, often narrow, mostly denticulate, the costa prominent with numerous lateral veins; petiole mostly present; stipules mostly present, deciduous or persistent, sometimes foliaceous; buds with an indurate, deciduous scale and a hyaline membranous covering. *Inflorescences* dense spikes or racemes (aments, catkins), terminal on axillary shoots, lax or erect, subtended by basal leafy bracts; pedicels short, elongating in fruit, subtended by a bracteole. *Male flowers* with 1–2 short glands above the bracteole or a disc, the stamens 2–8, the filaments free or basally united, sometimes pubescent, the anthers rotund, 2-thecate, longitudinally dehiscent; *female flowers* with short glands above the bracteole or surrounding the ovary, the ovary sessile or stalked, 1-loculed, the style short or elongate, the stigmas 2–4, short, digitate. *Fruit* a small, 2–4-valved capsule, the valves somewhat leathery, apically dehiscent and recurving; seeds numerous, lenticulate, long-pilose, the embryo erect with 2 large cotyledons and a short epicotyl, the endosperm nuclear.

Salix is a genus of over 500 species, widespread except in Australia and the South Pacific. In north temperate regions, species of *Salix* are frequently the dominant species, especially along watercourses and in marshes and other wet places. *Salix* wood is used in some countries for basketry, for building dykes and locks and for support for mud-covered houses. Trees are often fast growing.

1. **Salix humboldtiana** Willd., Sp. Pl., ed. 4. 657. 1805. TYPE: Peru, *Humboldt* (B-Willd. 18108, not seen, microfiche MO).

S. *chilensis* sensu auct., an Molina, Saggio Storia Nat. Chili 169. 1782.

Shrubs or *trees* to 15 m tall; branches slender, flexuous, puberulent with weak spreading hairs, drying with reddish bark, the youngest growth drying yellowish.

FIGURE 1. *Salix humboldtiana* Willd.—A. Flowering branch (×3/5).—B. Single flower, female (×8 9/10). [After *Tyson* 7379 (MO).]

Leaves linear-lanceolate, 5–6 cm long, 4–6 mm wide, apically acute, basally obtuse, the margins serrate with low callose-glandular teeth, glabrous beneath, the costa pilose to puberulent and glabrescent above, the costa prominently elevated beneath, plane above, the surface finely rugose above, the minor venation not evident, beneath the minor venation slightly elevated, differing in texture from above, the lateral veins ill-spaced, more or less arcuate, forming a well-defined submarginal vein ca. 0.5 mm from the margin; petiole slender, 3–5 mm long, deeply canaliculate above, pubescent; stipules subfoliaceous, dentately 3–4 mm long, deciduous. *Inflorescences* lax racemes (aments, catkins) terminal on short lateral shoots, 3–10 cm long, the flowers congested at anthesis, slightly more distant in fruit, the rachis angled, short-pilose near the base with several foliose basal bracts with reduced stipules; bracteoles 1–2 mm long, ovate, densely ciliate; pedicels obsolete. *Flowers* (female) with the gland deeply 2-lobed, ca. 0.3 mm long, slightly reddish; ovary narrowly ellipsoidal, stipitate, the stipe 0.5–1.0 mm long, in fruit becoming 1 mm long and resembling pedicels, the stigmas 4 in 2 pairs, digitate. *Fruit* ovoid to ellipsoidal, ca. 6 mm long, drying brownish; seeds ca. 1 mm long, compressed trapezoidal, long pubescent (comose) with white hairs. Male flowers were not seen.

This species is distinct in the Panamanian flora because of its narrow, serrate leaves and its racemes of small fruits filled with silky-plumose seeds. In Panama it has been collected only in the Chiriquí Mountains. *Salix humboldtiana* ranges widely in South America and through Central America into Mexico. Becoming a substantial tree, it is also widely cultivated in warm parts of the New World.

This species belongs (Schneider, 1919) to sect. *Nigrae* of the *Pleiandrae* group, which includes sects. *Nigrae*, *Triandrae*, and *Pentandrae* subsects. *Lucidae* and *Bonplandianae*. This group is entirely New World in occurrence, ranging from Ontario to South America. In this group male flowers have 3–15 stamens whereas other American species in the genus have 2 or only 1. A number of infraspecific taxa have been recognized under S. *humboldtiana*.

Although the name S. *chilensis* is earlier than the name used here, Schneider (1917) dismissed it, judging that it probably does not refer to a member of this genus. Common names are "sauce" (Spanish); "willow" (English).

CHIRIQUÍ: In village of El Volcán, 4,000 ft, *Tyson 7379* (MO).

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FLORA OF PANAMA[1]

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part VI

FAMILY 99. BUXACEAE

ALWYN H. GENTRY[2]

Trees, *shrubs*, or rarely *herbs*, monoecious or dioecious, usually glabrous, sometimes pubescent with simple trichomes. *Leaves* opposite or alternate, simple, usually entire, pinnately veined or 3-veined from the base, usually coriaceous, exstipulate. *Inflorescence* spicate to racemose, usually congested, axillary, bracteate. *Flowers* without petals; male flowers usually with 4 separate sepals and 4–6(–many) stamens, when 4, borne opposite sepals, the filaments lacking to conspicuous, the anthers often dorsifixed, 2-locular, longitudinally dehiscent or dehiscing by valves; female flowers usually few and larger than the male, the sepals 4–6, the ovary superior, 3-locular, the styles usually conspicuous, the ovules 1–2 per locule, pendulous, anatropous, with a ventral raphe. *Fruit* a loculicidally dehiscing capsule or drupe, the styles usually persistent and conspicuous, 1–few-seeded; seeds with endosperm, often black and shining, the embryo straight with flat or thick cotyledons.

A mostly north temperate family of 5 genera and about 100 species, the Buxaceae are usually allied to the Euphorbiaceae and sometimes reduced to a tribe of that family. They are placed in Hamamelidales by Hutchinson (1967). Two small New World genera, *Styloceras* (3 species of the northern Andes) and *Simmondsia* (1 species of the southwestern United States and adjacent Mexico) are accorded familial recognition by Airy Shaw (1966) and allied respectively with Didymeleaceae and Monimiaceae.

The family has some economic importance. *Buxus sempervirens* L. provides a dense compact wood and is much used as an ornamental hedge in formal gardens. *Pachysandra* is used horticulturally as a ground cover. *Styloceras* provides a potentially useful timber and the seeds of *Simmondsia* or jojoba are rich in natural wax with industrial possibilities.

Literature:

Airy Shaw, H. K. 1966. J. C. Willis. A Dictionary of the Flowering Plants and Ferns. Ed. 7. Cambridge Univ. Press, Cambridge.

Baillon, H. 1859. Monographie des Buxacées et des Stylocérées. Librairie de Victor Masson, Paris.

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[1] Assisted by National Science Foundation Grant DEB 77-04300, (W. G. D'Arcy, principal investigator).

[2] Missouri Botanical Garden, 2345 Tower Grove Avenue, St. Louis, Missouri 63110.

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Baldwin, J. & Collaborators. 1965. The relatives of *Buxus*. Boxwood Bull. 5: 17–36.
Hutchinson, J. 1967. The Genera of Flowering Plants. Vol. 2. Clarendon Press, Oxford.
Mathou, T. 1940. Recherches sur la famille des Buxacées, étude anatomique, microchimique et systématique. Douladoure, Toulouse.

1. BUXUS

Buxus L., Sp. Pl. 983. 1753; Gen. Pl., ed. 5. 423. 1754. TYPE: *B. sempervirens* L.

Crantzia Swartz, Prodr. Veg. Ind. Occ. 3: 38. 1788, non Scopoli, 1777, Gesneriaceae, nom. rejic. against *Alloplectus* Mart. TYPE: *C. laevigata* Swartz = *Buxus laevigata* (Swartz) Spreng.
Tricera Schreb., Gen. Pl. 630. 1791 (trim. 2). TYPE: *T. laevigata* (Swartz) Swartz = *Buxus laevigata* (Swartz) Spreng.
Notobuxus Oliv., Hooker's Icon. Pl. 14: 78, *tab. 1400*. 1882. TYPE: *N. natalensis* Oliv.
Macropodandra Gilg., Bot. Jahrb. Syst. 28: 114. 1899. TYPE: *M. acuminata* Gilg.

Monoecious *shrubs* or small *trees*. *Leaves* opposite, entire, coriaceous. *Inflorescences* axillary, racemose, congested, bracteate, usually with a single terminal female flower and several to many lateral male flowers. *Flowers* apetalous; male flowers with 4 sepals, the stamens 4–6, opposite the sepals, the filaments exserted, the anthers dorsifixed near the base; female flowers with 4–6 sepals, the ovary 3-locular with 3 distinct styles and 2 ovules per locule. *Fruit* a capsule, 3-parted, apically 3-horned from the persistent styles; seeds oblong, black.

Buxus includes about 70 species, mostly in the West Indies (sect. *Tricera*, primarily in Cuba and Jamaica, 33 species) and Eurasia (sect. *Buxus*); 10 species occur in Africa, (sect. *Buxella* and *Notobuxus*). Four species occur in Mexico, adjacent Guatemala, and Belize. Attempts to segregate the New World species as *Tricera*, characterized chiefly by the elongate style, are unjustified. African *Notobuxus*, separated by sessile anthers and lack of a rudimentary ovary in male flowers, also seems best referred to *Buxus* following Hutchinson (1967).

1. **Buxus citrifolia** (Willd.) Spreng., Syst. Veg. 3: 847. 1826.

Tricera citrifolia Willd., Sp. Pl., ed. 4. 4: 338. 1805. TYPE: Venezuela, *Bredemeyer* (not seen).

Monoecious *shrub* or small *tree* 3–5 m tall, to 5 cm d.b.h.; twigs glabrous, somewhat tetragonal, the angles ridged and prominent. *Leaves* elliptic to narrowly elliptic-ovate, more or less acuminate, cuneate to rounded at the base, entire, subcoriaceous or coriaceous, glabrous, 5–12 cm long, 2–5 cm wide, sub-3-veined from the base with the outer 2 nerves forming submarginal veins, the venation inconspicuous above, prominulous beneath, the petiole margined, 2–5 mm long. *Inflorescence* short, 1–2 cm long axillary, cymose-racemose with a single terminal female flower and several lateral male flowers; bracts triangular, 1–2 mm long, ciliate; pedicels of male flowers 2–4 mm long, the female flowers sessile. *Flowers* white, fragrant; calyx of male flowers petaloid, the 4 sepals obovate, 2–3 mm long, papillose-ciliate, the stamens 4, opposite the sepals, the filaments thick, 2–3 mm long, the terminal anther 0.5–1 mm long; female flower

FIGURE 1. *Buxus citrifolia* (Willd.) Spreng.—A. Flowering branch (×⅗).—B. Male flower (×5). [After *Nee & Hansen 14051* (MO)].—C. Fruit (×⅗). [After *Gentry 5029* (MO).]

with 6 ciliolate and somewhat puberulous biseriate sepals ca. 1.5 mm long, the ovary ca. 3 mm long with 3 styles 3–4 mm long. *Capsule* 3-valved and 3-horned from the persistent styles, 7–8 mm long not including the 5–7 mm long styles, loculicidally dehiscing so each valve 2-horned; seeds black, shiny, ca. 5 mm long, 1.5–2 mm wide.

In Panama this species is restricted to the limestone outcrop region of Central Panama where it is one of the characteristic elements, growing with such striking local endemics as *Parmentiera cereifera* Seem., *Capparis mirifica* Standley, and *Coccoloba* aff. *acapulcensis* Standley. Although I have not seen the type, the Panamanian material is a good match for the available material from Venezuela. A number of West Indian collections of this affinity have often been included under *B. citrifolia*, which has thus been cited from Martinique, Cuba, and Puerto Rico. The closely related Cuban and Puerto Rican plants differ in shorter more globose capsules with shorter horns and should be known respectively as *B. brevipes* (Müll.-Arg.) Urb. and *B. portoricensis* Alain or lumped under *B. laevigata* (Swartz) Spreng. The similar Martinique plant which has often been cited as *B. citrifolia* does have long capsule horns but was separated from *B. citrifolia* by Müll.-Arg. on account of fused style bases; its flowers are also larger than in *B. citrifolia*. *Buxus citrifolia* itself has sometimes been considered synonymous with the older *B. laevigata*, but topotypic material of *B. laevigata* from Jamaica differs in having smaller flowers and fruits and smaller, more broadly elliptic leaves with more pronounced secondary venation and more marginal lateral veins.

CANAL ZONE: Road to Battery VII, W of Gatún Locks, *Johnston 1774* (MO). Río Pequení, Salamanca Hydrographic Station, *Woodson et al. 1563* (MO). PANAMÁ: Icantí, Río Agua Clara, *Gentry 2604* (MO). Archaeological site at edge of Madden Lake, *Gentry 5029* (MO). Near Puente Natural SE of Madden Lake, *Nee & Hansen 14051* (MO). 5 mi above Majé, *Foster & Kennedy 2022* (MO).

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FLORA OF PANAMA[1]

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part VI

FAMILY 123A. HYPERICACEAE

NORMAN K. B. ROBSON[2]

Trees, *shrubs*, perennial or annual *herbs*, or rarely *lianas*, unarmed, glabrous or with simple, stellate or dendroid hairs, containing various secretions in schizogenous canals or locules. *Leaves* opposite, decussate or rarely the upper ones alternate, simple, entire or rarely gland fringed, sessile or petioled, often with translucent glandular dots, lines or with black or red glandular dots; stipules absent, but an interfoliar ridge often present. *Inflorescences* terminal and sometimes also axillary, rarely wholly axillary or cauliflorous, cymose to thyrsoid or racemose, 1–many-flowered; bracts and bracteoles present at least initially, sometimes reduced to ledges. *Flowers* bisexual, actinomorphic, radiate to cupulate or pseudotubular, homostylous or heterodistylous; sepals 5 and quincuncial or rarely 4 and decussate, free or united, imbricate, entire or with the margin variously divided, often glandular, the lamina glandular like the leaves, usually with more glands linear than punctiform, almost always persistent in fruit; petals 5 or rarely 4, free, imbricate (contorted), alternisepalous, entire or with the margin variously divided and often glandular, the lamina usually glandular like the leaves, sometimes with a nectariferous basal appendage, glabrous or adaxially villous, deciduous or persistent; stamen fascicles 5(4), antepetalous, free or variously united, each with 1–many stamens, the filaments variously united or apparently free, the free part slender, the anthers small, dorsifixed, usually with a gland terminating the connective, 2-thecal with thecae parallel, dehiscing longitudinally; staminodial fascicles 3 or 5 or absent, when present alternating with the stamen fascicles; ovary 1, superior, 3–5-locular or 1-locular with 2–5 parietal placentas, the ovules 1–many on each placenta, anatropous, horizontal or ascending, the styles (2–)3–5, free or united, elongate, slender, the stigmas punctiform to broadly capitate or rarely bifid. *Fruit* capsular, dehiscing septicidally or loculicidally, or baccate or rarely drupaceous with 5 pyrenes; seeds 1–many on each placenta, the testa often sculptured or gland dotted and sometimes winged or carinate, exarillate, rarely carunculate, without endosperm; embryo cylindric, straight or curved, the cotyledons longer to shorter than the hypocotyl, straight or rarely convolute.

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[1] Assisted by National Science Foundation Grant DEB 77-04300 (W. G. D'Arcy, principal investigator).

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ANN. MISSOURI BOT. GARD. 65: 9–26.

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The Hypericaceae is a family of 8 genera with about 500 species, of which about 400 belong to *Hypericum*. This is mainly a temperate genus but it occurs in mountains in the tropics. The other genera are wholly tropical in distribution, except for the East Asian and North American *Triadenum* Raf. Two genera are native to Panama. The type genus is *Hypericum* L.

The Hypericaceae is frequently included in the Guttiferae as subfamily Hypericoideae; and indeed it is no more distinct from the other subfamilies than they are from each other. However, the three hypericaceous tribes themselves, Vismieae, Cratoxyleae and Hypericeae, are not closely related; and so the traditional classification is adopted here for convenience rather than as a definitive scheme.

The Hypericaceae can be recognized by their simple, opposite, exstipulate leaves with usually punctiform glands, bisexual flowers usually with a 5-merous perianth, slender filaments and small anthers, and slender styles.

In general, the family has been used as a source of durable or easily worked woods and of drugs or dyes from the bark and leaves. *Hypericum* is much used in horticulture for the decorative value of many of its species. Certain species have proved troublesome in various parts of the world because they contain two naphthodianthrones, hypericin and pseudohypericin, which are photodynamically active and produce sores on browsing animals.

a. Herbs or shrublets; leaves (Panama) sessile, glabrous, 3–25 mm long; petals glabrous; styles 3; stamen filaments free to near the base; fruit capsular, 3-valved (Panama) ---- 1. *Hypericum*

aa. Shrubs or trees; leaves (Panama) petiolate, pubescent (or glabrescent) to tomentose beneath, 60–400 mm long; petals internally villous; styles 5; stamen filaments united in 5 fascicles; fruit baccate, 5-locular ---------- 2. *Vismia*

1. HYPERICUM

Hypericum L., Sp. Pl. 783. 1753; Gen. Pl., ed. 5. 341. 1754. TYPE: *H. perforatum* L.[3]

Trees, *shrubs* or perennial to annual *herbs*, glabrous or with simple hairs, with glandular canals or locules containing resins (amber), essential oils (pellucid) and often hypericin and pseudohypericin (black or red). *Leaves* opposite, entire, rarely gland fringed, sessile or shortly petiolate, the venation subparallel or variously reticulate, pellucid or dark glands present on lamina or margins. *Inflorescences* 1–many-flowered, usually dichasial, terminal and sometimes also axillary, with branches regularly bracteate and bracteolate, sometimes foliate; the bracts often foliaceous; pedicels usually present. *Flowers* homostylous or rarely heterostylous, the perianth usually radiate to cupulate; sepals 5, quincuncial, or occasionally 4 and decussate, glandular like the leaves; petals 5(4), contorted in bud, yellow to orange or rarely white, often tinged or veined with red in areas exposed in bud, usually asymmetric, variously glandular, deciduous or persistent, glabrous; stamen fascicles free, variously united or sometimes apparently absent, deciduous or persistent, glabrous, each with many to few

[3] A list of generic and subgeneric synonyms will be found in Robson (1977). The two Panamanian species belong to sect. *Spachium* (R. Keller) N. Robson.

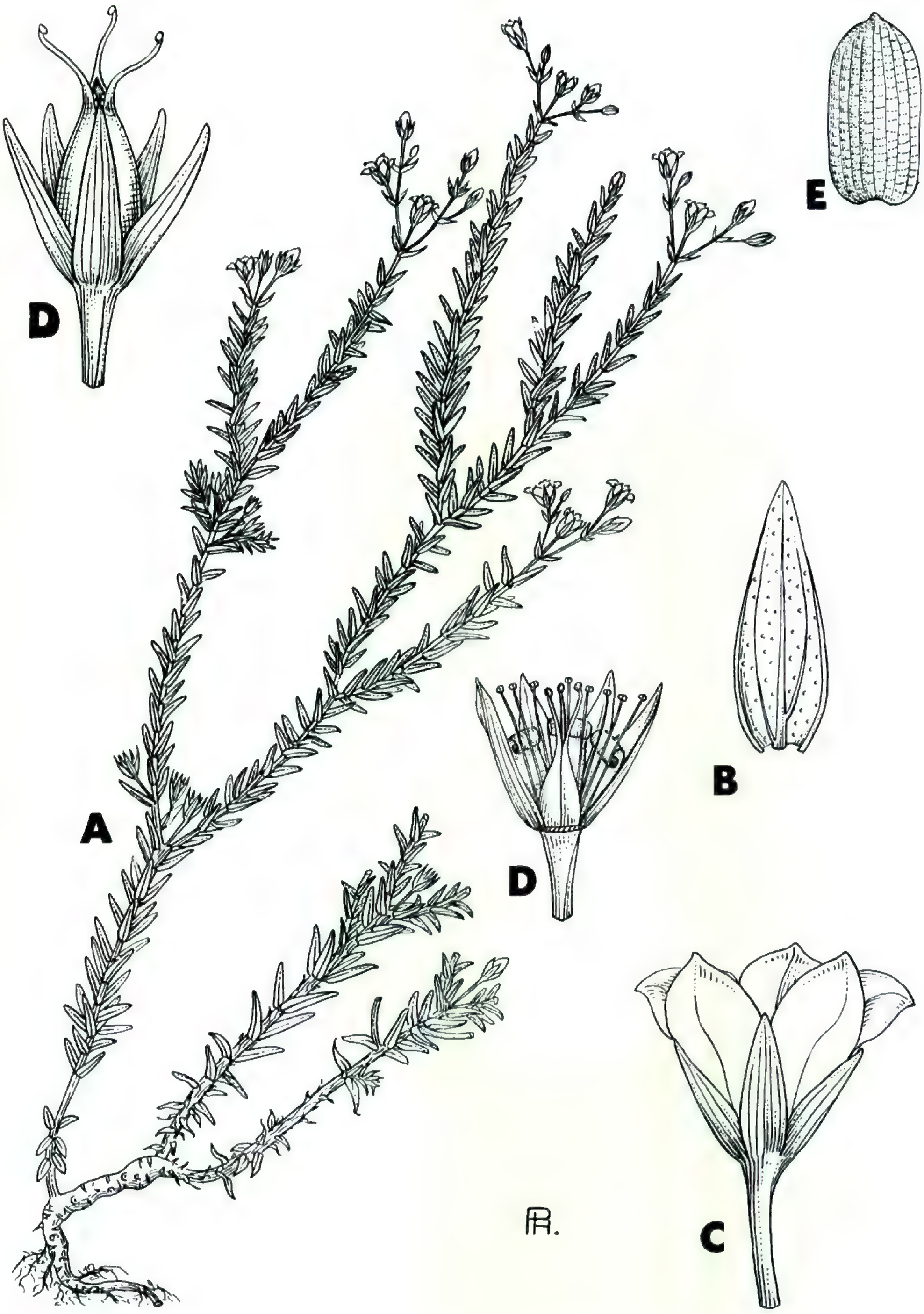

FIGURE 1. *Hypericum gnidioides* Seem.—A. Habit (×3⅗).—B. Leaf underside (×2⁹⁄₁₀).—C. Flower (×3⁹⁄₁₀).—D. Flower with 2 petals, 1 sepal and some stamens removed (×3⁹⁄₁₀). [After *Tyson 5713* (MO).]—E. Fruit (×3⁹⁄₁₀).—F. Seed (×35). [After *Lazor & Correa 2703* (MO).]

stamens, or rarely reduced to 1 stamen, the filament slender, usually free almost to the base, the anther oblong or elliptic with an amber or dark gland on the connective; staminodial fascicles absent or rarely 3, glabrous; ovary glabrous, 3–5-locular with axile placentas or completely unilocular with (2–)3–5 parietal placentas, each placenta with 2–many ovules, the styles (2–)3–5, free or partly to completely united, glabrous, the stigma small or broadly capitate. *Fruit* a septicidal capsule, occasionally fleshy and tardily dehiscent, the (2–)3–5 valves often with resin-containing vittae or vesicles, 1–many-seeded; seeds small, the testa variously sculptured, often carinate or winged, the embryo slender, straight, with distinct straight cotyledons.

Hypericum is a genus of ca. 400 species distributed throughout most mesophytic parts of the world except the lowland tropics, but most abundant in temperate regions. The least specialized species are arborescent and occur in Africa, but most of the genus consists of shrubs or perennial herbs.

Many species of *Hypericum* are cultivated in other countries, mostly as flowering shrubs or alpines. Otherwise the main economic importance of the genus derives from its contained hypericin, which renders hairless parts of the muzzles of browsing animals photosensitive, producing "hypericism," an often fatal condition.

Literature:

Robson, N. K. B. 1977. Studies in the genus *Hypericum* L. (Guttiferae). 1. Infrageneric classification. Bull. Brit. Mus. (Nat. Hist.), Bot. 5: 293–347.

Rodríguez Jiménez, C. 1975. Recherches sur *Hypericum* L. section *Brathys* (Mutis ex L.f.) Choisy sous-section *Spachium* Keller (Guttiferae). Mem. Soc. Ci. Nat. La Salle 33: 5–151.

a. Shrublet; all internodes shorter than the leaves; leaves coriaceous; inflorescence mostly monochasial or mixed bracteate and foliate, not regularly dichasial; styles 1.3–1.5 times as long as the ovary; capsule shorter than the sepals ..... 1. *H. gnidioides*

aa. Perennial to annual herb; upper internodes longer than the leaves; leaves coriaceous; inflorescence usually regularly dichasial at first, becoming monochasial; styles not longer than the ovary; capsule 1.3–2.0 times as long as the sepals ..... 2. *H. silenoides*

1. **Hypericum gnidioides** Seem., Bot. Voy. Herald 88, *tab. 17*. 1853. TYPE: Panama, *Seemann* (GOET, lectotype; BM, F, K, NY, isolectotypes; US, photo).

H. woodsonii Standley, Ann. Missouri Bot. Gard. 26: 294. 1939. TYPE: Panama, *Woodson et al. 1040* (F, MO, NY, US).

H. pinetorum Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 23: 65. 1944. TYPE: Honduras, Dept. Comoyagua, near Siguatepec, *Standley 55880* (F).

H. arbuscula sensu Rodríguez-Jiménez, Mem. Soc. Ci. Nat. La Salle 33: 114. 1975, non Standley & Steyermark, 1944.

Glabrous *shrublet* 3–55 cm tall with a taproot, usually bushy with the branches erect, strict or the lower ones ascending, rarely decumbent and matforming, not rooting at the base; stems 4-lined at first, eventually terete, sparsely gland dotted with the internodes shorter than the leaves. *Leaves* sessile, erect or suberect, usually imbricate, coriaceous, subconcolorous; lamina (3–)8–14(–18) mm long, 0.8–3.5(–5.0) mm wide, linear, elliptic-oblong, lanceolate or rarely ovate-

lanceolate, the apex acute, the margin entire, revolute, the base parallel to narrowly cuneate, the lateral vein pairs 0–3, without reticulate venation, the laminar glands pellucid, punctiform, dense, large, more prominent beneath, the marginal glands absent, the upper epidermal cells bullate. *Inflorescences* 1–25-flowered, monochasial after the first or second grade, with foliate and bracteate branches mixed, or wholly foliate, without subsidiary inflorescence branches; pedicels 4–10 mm long in fruit; bracts and bracteoles mostly foliaceous when present. *Flowers* 0.6–1.0 cm (or larger?) in diameter; sepals 4–8 mm long, 1.0–2.3 mm wide, unequal, oblanceolate-spatulate, oblong, elliptic to linear, acute, 5-nerved, the nerves prominent; petals bright yellow to orange, 5.0–8.5 mm long, 3–6 mm wide, slightly exceeding the sepals, obovate to oblong; stamens 20–40, not fascicled, the longest 3.5–6.0 mm long, ¾ times as long as the petals, the anther gland amber; ovary 1.5–1.8 mm long, 0.6–1.0 mm wide, narrowly ovoid-ellipsoid, the styles 3, 2–3(–4) mm long, 1.3–1.5 times as long as the ovary, the stigmas broadly capitate, the placentas 3, parietal with numerous ovules. *Fruits* 3.5–5.0 mm long, 2–3 mm wide, narrowly ovoid to cylindric, trigonous, acute to subacuminate, shorter than the sepals; seeds ca. 0.6 mm long, cylindric, longitudinally ribbed with transverse striae.

Hypericum gnidioides occurs from Panama northward to Mexico (Mexico and Guerrero), its nearest ancestral species being apparently *H. chamaemyrtus* Tr. & Pl. of Colombia. In Panama, it is found at higher altitudes in the Chiriquí mountains (1,100–3,475 m) and there is one record from Coclé Province (1,000 m). It occurs in savannas and grasslands, especially on old lava flows. At exposed sites on the highest part of its range (2,500–3,475 m) it adopts a decumbent matlike form (*H. woodsonii*), but this is only an extreme variant, not a distinct taxon.

CHIRIQUÍ: Slopes of Volcán de Chiriquí and along Río Chiriquí Viejo, 1,200 m, *Allen 1002* (MO). 5 km NW of Hato del Volcán, *Correa 1368* (DUKE, MO). 1 mi N of El Hato del Volcán, *Croat 10688* (MO). Alto Respinga and above, 2,800 m, *D'Arcy 9939* (BM, MO). Between El Hato and Bambito, *D'Arcy 10045* (BM, MO). On very top of El Baru, 3,475 m, *D'Arcy 10180* (BM, MO). Ca. 3 km NE of El Hato del Volcán, 1,500–1,800 m, *Davidse & D'Arcy 10357* (BM, MO). Boquete, *Davidson 639* (F, MO). Volcán de Chiriquí, Potrero Muleto, 10,400 ft, *Davidson 1048* (F, MO). Boquete, Volcán de Chiriquí peak, *Davidson 1355* (F). Near town of Volcán, 4,600 ft, *Duke 9156* (MO). Llanos region, El Volcán, *Ebinger 777* (F, MO, US). Piedro de Lino, 1,600 m, *Killip 3575* (US). ½ mi S of Bambito, *Lazor & Correa 2703* (MO). W slopes of Volcán de Chiriquí (Baru), *Mori & Kallunki 5688, 5761* (both MO). 1 mi S of Bambito, *Partch 69-22* (MO). Alto Boquete, 1,125 m, *Partch 69-44, 69-74* (both MO). Above Boquete, foot of Cerro de Lino, 1,300–1,500 m, *Pittier 3035* (US). Chiriquí Volcán, N slope, 3,000–3,374 m, *Pittier 3092* (BM, NY, US). El Boquete, 700–1,100 m, *Pittier 3320* (US). Volcán de Chiriquí, *Sapper* Apr. 1899 (US). Volcano of Chiriquí, *Seemann 1640* (BM, GOET, K). Llanos de Volcán, *Seibert 349* (K, MO, NY). Boquete, Llanos Francia, 3,300 ft, *Stern et al. 1207* (MO, US). Boquete, Llanos area just S of the town, 3,500 ft, *Stern et al. 1934* (MICH, MO, US). 8 mi NE of El Volcán, 8,100–8,400 ft, *Tyson 845, 846* (both DUKE). Nueva California, 4,000 ft, *Tyson 5713* (MO). 3 mi N of El Volcán, 5,000 ft, *Tyson 5740* (MO). Top of El Baru, above 11,000 ft, *Tyson & Loftin 6159* (MO). Above gorge of Río Chiriquí, ca. 1.5 km, E of Panama Road 13, *Utley et al. 255* (DUKE). 6 km W of Cerro Punta, Las Nubes, 6,000–7,200 ft, *Wilbur & Almeda 17080* (DUKE). 4 km N of El Hato del Volcán, 1,400–1,600 m, *Wilbur & Luteyn 19416* (DUKE). Between Volcán Chiriquí and Cerro Aquacate, 6,500–7,200 ft, *Wilbur & Teeri 13310* (DUKE, F, MICH, MO). About halfway between Cerro Punta and Bambito, ca. 5,600 ft, *Wilbur et al. 10905* (DUKE). NE of El Hato, near Aguacate, 1,800–1,900 m, *Wilbur et al. 10977* (DUKE).

5 km NE of El Hato toward Volcán de Chiriquí, *Wilbur et al. 11858* (DUKE). 4 km NE of El Hato near Río Macho de Monte, 1,800 m, *Wilbur et al. 13060* (DUKE). 2 mi NE of El Hato del Volcán, ca. 1,500 m, *Wilbur et al. 15305* (DUKE). Between El Hato and Volcán de Chiriquí, *Wilbur et al. 15410* (DUKE). Volcán Chiriquí, Loma Larga to summit, 2,500–3,380 m, *Woodson et al. 1040* (F, MO), *1074* (MO, NY). Volcán de Chiriquí, Casita Alta to Cerro Copete, 2,300–3,300 m, *Woodson & Schery 374* (F, MO). Volcán de Chiriquí, Potrero Muleto to summit, 3,500–4,000 m, *Woodson & Schery 424, 430* (both F, MO). Boquete, *Woodson & Schery* 772 (MO, US). COCLÉ: El Valle de Antón, ca. 2 mi W of town, 1,000 m, *Luteyn 1262* (DUKE). Between Las Margaritas and El Valle, *Woodson et al. 1758* (F, MO).

2. **Hypericum silenoides** Juss., Ann. Mus. Natl. Hist. Nat. 3: 162, *tab. 16, fig. 3.* 1804. TYPE: Peru, *Dombey* (P; photo, F).

H. thesiifolium H.B.K., Nov. Gen. Sp. Pl. 5: 192. 1822. TYPE: Colombia, *Humboldt & Bonpland* (P).
H. uliginosum H.B.K., Nov. Gen. Sp. Pl. 5: 194. 1822. TYPE: Venezuela, *Humboldt & Bonpland* (P).

Short-lived perennial (?) or annual *herb*, glabrous, 8–45 cm tall, with taproot, caespitose; branches erect or decumbent, not rooting at the base; stems 4-lined, flattened above, densely pellucid-gland-streaked, the lower internodes shorter than the leaves, the upper ones to 2 times as long as the leaves. *Leaves* sessile, erect or more rarely spreading, not or scarcely imbricate, chartaceous, paler beneath; lamina 7–25 mm long, 1.5–6.0 mm wide, linear to elliptic-oblong or lanceolate, the apex acute to subacute, the margin entire, plane or sometimes revolute, the base narrowly to broadly cuneate, the lateral vein pairs 0–3, without or with obscure reticulate venation, the laminar glands punctiform to linear, large to small, more prominent beneath, the marginal glands present or absent, the upper epidermal cells subbullate. *Inflorescences* 1–many-flowered, regularly dichasial or partly monochasial, rarely with some foliate branches from the uppermost node, frequently with subsidiary inflorescence branches from the lower nodes; pedicels 1–7 mm long in fruit; bracts and bracteoles foliaceous but smaller to subulate. *Flowers* 0.4–1.0 cm in diameter; sepals 3.0–5.5 mm long, 0.5–1.4 mm wide, unequal, lanceolate, oblong-elliptic or linear, acute to subacute, 3–7-nerved, with the nerves scarcely prominent; petals deep yellow to orange, 4.0–6.5 mm long, 1.5–2.0 mm wide, ca. 1.3–2.0 times as long as the sepals, obovate; stamens 12–30, irregularly grouped, the longest 3.0–5.5 mm long, ca. ½–¾ times as long as the petals, the anther gland amber; ovary 1.5–2.0 mm long, 0.7–1.0 mm wide, narrowly ovoid-ellipsoid, the styles 3, 1.0–1.5 mm long, ca. 0.75–1.0 times as long as the ovary, the stigmas broadly capitate, the placentas 3, parietal, with many ovules. *Fruits* 5–7 mm long, 1.5–3.0 mm wide, narrowly cylindric or ovoid-cylindric, acute to obtuse, ca. 1.3–2.0 times as long as the sepals; seeds ca. 0.6 mm long, cylindric, longitudinally ribbed-scalariform.

Hypericum silenoides sensu lato occurs along the Cordillera from northwest Argentina to central Mexico, as well as in the Galapagos and Revilla Gigedo Islands. Although it shows considerable variation in habit, leaf width, and flower and fruit size throughout this wide range, and hence has numerous synonyms (see Rodríguez Jiménez, 1975), the variation is apparently continuous, with the possible exception of a small-flowered population in mainland Ecuador and the Galapagos Islands. In Panama it is found only in the Chiriquí mountains, 1,100–

2,400 m, where it grows in various open habitats: roadsides, streamsides, open woodland.

CHIRIQUÍ: "New Switzerland," central valley of Río Chiriquí Viejo, 1,800–2,000 m, *Allen 1368* (MO, NY). 5.4 km from Hato del Volcán towards Las Lagunas, *Correa & Lazor 1514* (DUKE, MO). Trail N of Cerro Punta, *Croat 10453A* (MO). Volcán District, near Las Lagunas, *D'Arcy 10060* (BM, MO). Across river from Cerro Punta, *D'Arcy & D'Arcy 6538* (MO). Boquete, 3,800 ft, *Davidson 602* (F, MO). Boquete, 7,000 ft, *Davidson 893* (US). El Hato de Volcán, *Ebinger 769* (F, MO). Between El Hato and Costa Rica, *Ebinger 819* (F, MO, US). 1.6 mi NW of El Hato de Volcán towards Costa Rican border, *Luteyn 817* (DUKE). NE of El Hato del Volcán, ca. 6,200 ft, *Luteyn & Utley 17212* (DUKE). Llanos de Volcán, 1,120–1,200 m, *Seibert 347* (MO). Cerro Punta, 6,000 ft, *Tyson 5813* (DUKE, MO). Valley of upper Río Chiriquí Viejo, *White 10* (MO). Between Cerro Punta and Las Nubes, *Wilbur & Teeri 13247* (DUKE). ½ mi from El Hato del Volcán, *Wilbur et al. 11946* (DUKE). Río Chiriquí valley, E of Guadeloupe, ca. 6,500 ft, *Wilbur et al. 13029* (DUKE). Ca. 5 km NW of Cerro Punta, *Wilbur et al. 15193* (DUKE). Volcán de Chiriquí, vicinity of Casita Alta, 1,500–2,000 m, *Woodson et al. 849* (F, MO, NY). Finca Lerida to Peña Blanca, 1,750–2,000 m, *Woodson & Schery 299* (MO).

2. VISMIA

Vismia Vandelli, Fl. Lusit. Bras. Sp. 51, *tab. 3, fig. 24.* 1788, nom. cons. TYPE: *V. cayennensis* (Jacq.) Pers.

Caopis Adans., Fam. Pl. 2: 448, 531. 1763, nom. rejic.

Trees or *shrubs* with simple and also stellate or dendroid hairs, glandular canals containing yellow to orange resinous sap, and glandular loculi or vittae containing amber or black secretions. *Leaves* opposite, entire, petiolate or rarely sessile, the secondary venation pinnate, the tertiary venation reticulate, the lamina often with dark glands, usually densely pubescent or tomentose beneath. *Inflorescences* many–2-flowered, usually thyrsoid, terminal and often also axillary, rarely only axillary or cauliflorous; bracts and bracteoles represented by tomentose ledges; pedicels present. *Flowers* homostylous or dimorphically heterostylous, the perianth erect; sepals 5, quincuncial, the outer parts thick in bud, usually tomentose, the inner parts thin in bud, often scarious, glandular-vittate or -punctate; petals 5, white or greenish white to yellow, asymmetric or not, eglandular or variously glandular-vittate or -punctate, deciduous, externally glabrous, internally whitish-villous; stamen fascicles free or rarely united with the petals, glabrous or villous, deciduous or persistent, each with many–3 stamens, the filaments slender, more than half united, the anthers ovoid or globose with an amber (? or dark) gland on the connective; staminodial fascicles 5, glabrous or pilose, alternating with the stamen fascicles; ovary glabrous, 5-locular with axile placentas, each placenta with many–5 ovules, the styles 5, free or coherent below but not united, sometimes hirsute, the stigma broadly capitate to recurved-bifid. *Fruit* a smooth glabrous berry with fleshy pericarp, or thin pericarp, and then 5-lobed and sometimes apparently capsular when dried, often glandular-punctate, many seeded; seeds small with the testa finely reticulate, not or scarcely carinate, the embryo slender, straight, with distinct straight cotyledons.

A genus of about 55 species in lowland and upland regions, 6 in tropical Africa and the rest in tropical America, the least specialized species are Amazonian.

Vismia contains no species of great commercial value, but the yellow, orange, or red sap is used in local folk medicines, as is juice from the bark, which is also said to serve as a fish poison.

In addition to the species noted below, *V. baccifera* (L.) Triana & Planch. (1862) (= *V. mexicana* Schlecht.), the type of which is Mexican, is quite common in Costa Rica. No certain records of this species for Panama exist, but a sterile collection from Chiriquí [Panamerican Highway ca. 8 km N of Camp El Volcán, *Little 6052* (MO)] may belong to it. *Vismia baccifera* can be distinguished from *V. panamensis* by the chocolate to brown (not ferrugineous to fawn) indumentum, which soon turns grayish, the abruptly acuminate leaves, the longer pedicels (4–7 mm), the homostylous flowers, the paler petals (white to cream yellow, not pale to golden yellow), and the fruit, which is usually described as black, whereas in nearly all collections of *V. panamensis* it is said to be green.

Literature:

Ewan, J. 1962. Synopsis of the South American species of *Vismia* (Guttiferae). Contr. U.S. Natl. Herb. 35: 293–373.

a. Stamen and staminodial fascicles persistent in fruit; lower epidermis of leaf papillose, not obscured by a spreading indumentum; petals narrowly oblong-lanceolate, glandular-dotted; leaf lamina often over 20 cm long, with the base usually deeply cordate ..... 4. *V. macrophylla*

aa. Stamen and staminodial fascicles deciduous after flowering; lower epidermis of leaf smooth, glabrate or obscured by an appressed indumentum; petals obovate to oblanceolate, glandular-dotted to -lined or rarely eglandular; leaf lamina rarely over 20 cm long, with the base cuneate to rounded or rarely shallowly cordate.

b. Petals glandular lined or rarely eglandular; sepals erect to subreflexed in fruit; leaves coriaceous to thickly chartaceous, mostly ovate to lanceolate, ferrugineous to whitish beneath.

c. Leaves obtuse or abruptly acuminate; outermost sepals ovate, obtuse, 4–7 mm wide; inner margins of sepals entire or almost so; flowers homostylous ..... 3. *V. latisepala*

cc. Leaves gradually acuminate; outermost sepals oblong or elliptic to lanceolate, usually acute, 2.0–3.5 mm wide; inner margins of sepals ciliate; flowers homo- or heterostylous.

d. Flowers homostylous; sepals with the inner margins wholly ciliate; leaves rufous to dark brown beneath, at least the lower ones long-acuminate; fruits purplish ..... 2. *V. jefensis*

dd. Flowers heterostylous; sepals with the inner margins apically ciliate; leaves ferrugineous to fawn or rarely whitish or greenish beneath, acute or shortly acuminate; fruits green to black ..... 5. *V. panamensis*

bb. Petals glandular-dotted only; sepals strongly reflexed in fruit; leaves thinly chartaceous, mostly elliptic, ferrugineous to green beneath ..... 1. *V. billbergiana*

1. **Vismia billbergiana** Beurl., Kongl. Vetensk. Acad. Nya Handl. 1854: 117. 1856. TYPE: Panama, "in montis Portobelo," *Billberg 231* (S).

V. guianensis sensu Seem., Bot. Voy. Herald 88. 1853, non *V. guianensis* (Aubl.) Choisy.
V. viridiflora Duchass. ex Triana & Planch., Ann. Sci. Nat. Bot., sér. 4, 17: 302. 1862. LECTOTYPE: Panama, *Duchassaing* (GOET).

Shrub or *tree*, 1.5–8.0(–12.0) m tall, slender; bark rufous, flaking; sap orange; branches densely to sparsely ferruginous- to grayish-tomentose, pubescent with mostly appressed stellate hairs, glabrescent. *Leaves* petiolate; petiole 7–15 m

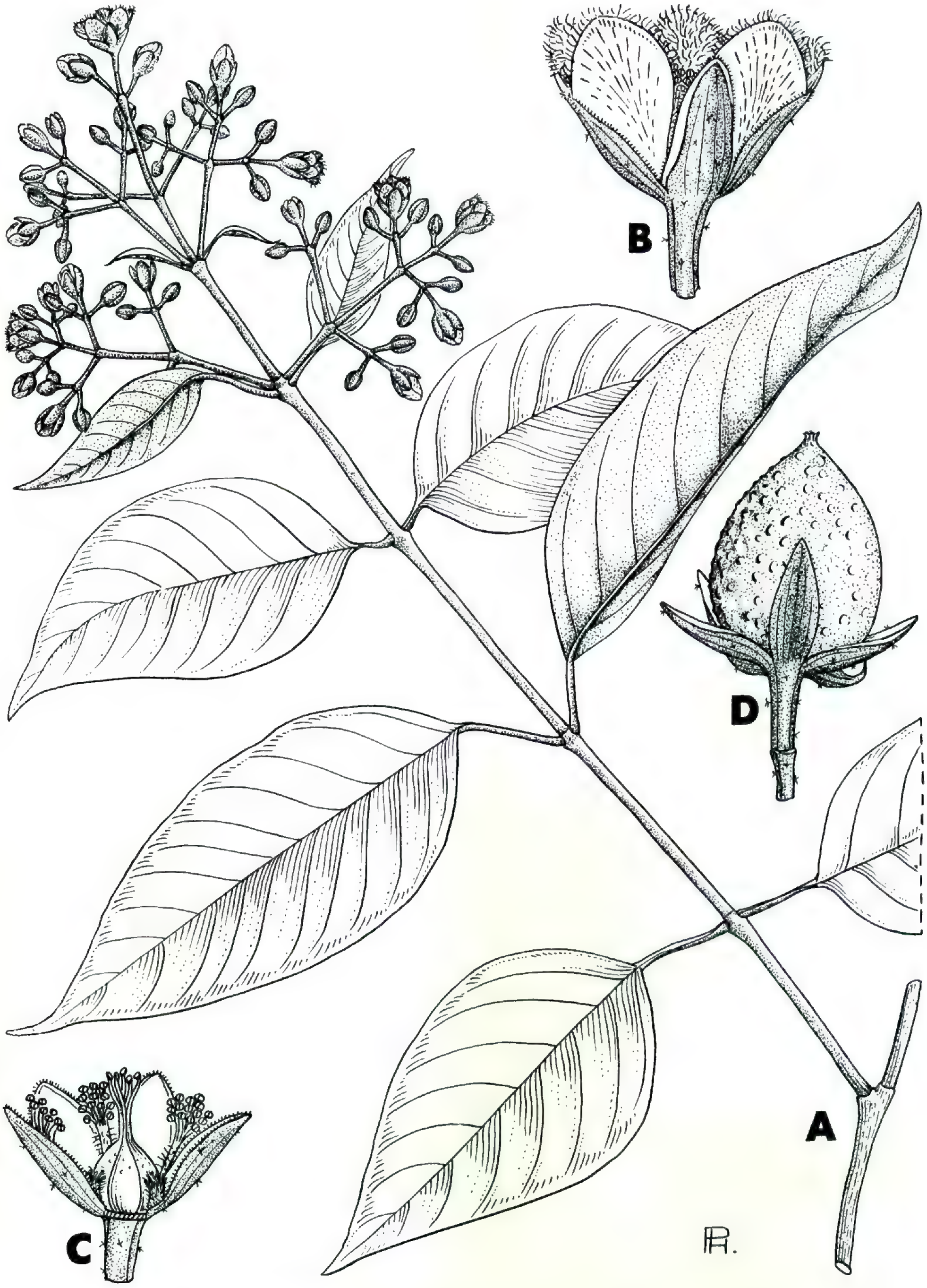

FIGURE 2. *Vismia jefensis* N. Robson.—A. Habit (×7/10).—B. Flower (×3).—C. Flower with part of perianth and 2 bundles of stamens removed (×3). [After *Correa & Dressler* 568 (MO).]—D. Fruit (×2). [After *Dwyer* 3378 (MO).]

long, ferrugineous- to grayish-tomentose or -pubescent, glabrescent; lamina (6.0–) 7.0–19.0 cm long, 1.5–9.6(–11.4) cm wide, broadly ovate to elliptic or lanceolate, the apex long-acuminate, to 30 mm long, the base rounded to narrowly cuneate, sometimes slightly asymmetric, thinly chartaceous, dull or sublucent above, bronze or orange brown to greenish beneath, the main lateral veins 7–12, orange to reddish, uniting in submarginal loops, sometimes with 1–3(–4) short intermediate lateral veins, with obscure reticulate venation slightly prominent on both sides, the glandular dots dense, sometimes obscure, the ferrugineous to whitish stellate hairs dense to sparse, closely appressed, often obscuring the smooth epidermis. *Inflorescences* terminal and sometimes axillary, 4–many-flowered, broadly pyramidal to subcylindric, 3–5-noded, the basal 1–2 nodes with deciduous bract pairs, the leaves at the node below scarcely reduced, sometimes bearing axillary accessory branches; rachis and pedicels ferrugineous to fawn appressed-tomentose, glabrescent; buds globose. *Flowers* heterostylous; sepals 5–7 mm long, united at the base, the outermost 2.0–3.5 mm wide, narrowly oblong to obovate-oblanceolate, obtuse to acute, exposed surfaces densely fawn- to ferrugineous-tomentose with appressed stellate hairs, the inner margins entire, sometimes ciliate, with few to numerous glandular dots, strongly reflexed in fruit; petals white or pale green to pale yellow, 7–10 mm long, 2.5–4.0 mm wide, 1.5–2.0 times as long as the sepals, oblanceolate to narrowly obovate, obtuse or rarely acute to rounded, distally reddish- or orange-glandular-punctate with large glands, internally whitish-villous; stamen fascicles united basally with the petals, deciduous, 14–20 stamens, whitish-villous, as long as the sepals (dolichostyly) or ca. 2 mm shorter than the petals (brachystyly); staminodial fascicles deciduous, ca. 1.5 mm long, oblong, distally pilose; ovary 2.0–2.5 mm long, globose, glandular-punctate, glabrous, the styles equaling the sepals (brachystyly) or ca. 2 mm short of the petal apex (dolichostyly), the stigmas broadly capitate to narrowly peltate. *Fruits* reddish purple with orange glandular dots, 8–13 mm long, 7–12 mm wide, globose to cylindric-globose, glabrous; seeds dark red brown, 3–4 mm long.

Vismia billbergiana appears to be derived from *V. sessilifolia* (Aubl.) DC., a species of the Guianas, adjacent Venezuela and Brazil, which differs mainly in having larger flowers and larger, oblong or elliptic-oblong leaves which are reddish, glabrous beneath, and sometimes sessile. It is confined to Costa Rica, Colombia, and Panama, where it grows in wet forest, woods, and thickets from sea level to 1,100 m.

Typical *V. billbergiana* has ovate to broadly elliptic leaves with a bronze to orange brown indument that obscures the lower epidermis, whereas typical *V. viridiflora* has narrowly elliptic to lanceolate or oblong-lanceolate leaves with a sparser indumentum that does not obscure the greenish lower epidermis. The sepals in fruit are typically spreading or somewhat reflexed in *V. billbergiana* and markedly reflexed in *V. viridiflora*. There is, however, a continuous series of intermediate specimens linking these extreme conditions. No other distinguishing characters, morphological, ecological, or distributional, appear to exist, and so the complex must be treated as one variable species.

BOCAS DEL TORO: Fish Creek Lowlands, Chiriquí Lagoon, *Wedel 2383* (MO). CANAL ZONE: Near Frijoles, *Allen 927* (BM, MO, NY). Río Chagrés above Gamboa, Juan Mina

plantation, *Allen 4146* (MO, NY). Pipeline Road, *Croat 4690* (DUKE, F, MO, NY), *9364* (F, MO), *13945* (MO). Along road to Gamboa airport, *Croat 14601a* (MO). Ancón Hill, *Duke 4608* (MO). Road C-21, *Duke 5792* (MO). Albrook, U.S. Army Tropic Test Center, *Dwyer & Robyns 86* (MO). Gamboa Naval Reservation, *Ebinger 900* (MO). Chagrés, *Fendler 6* (BM, K, MO). Gatún, *Hayes 433, 564, 569* (all NY); *Hladik 238* (NY). Summit Gardens, *Holdridge 6250* (DUKE, MO). W of Limón Bay, Gatún Locks and Gatún Lake, *Johnston 1604* (MO). Between Gamboa and Summit Gardens, *Kennedy 2258* (MO). Pipeline Road, *Lewis et al. 5459* (MO, NY). Near Bohio, *Maxon 4774* (MO). ½ km W of Gamboa, *Nee 9533* (MO). Río Mendosa, 9 km NW of Gamboa, *Nee 9573* (MO). Pipeline Road, 9 km NW of Gamboa, *Nee & Berg 8813* (MO). Chiva-Chiva Trail, *Piper 5763* (BM). Colón, along Río Fató, *Pittier 3876* (F). Río Tapia, *Standley 30688* (K). Darién Station, *Standley 31623* (BM). 6 mi N of Gamboa, *Tyson 1504* (DUKE, MO). Isthmus of Panama, *Weddell* (F). Ancón Hill, *Williams 7* (NY). BARRO COLORADO ISLAND: *Aviles 98b* (MO); *Brown 113* (F); *Croat 4693* (MO), *4751* (F, MO), *4844* (MO), *5089* (DUKE, F, MO, NY), *5586* (MO, NY), *5628* (MO), *7206* (F, MO, NY), *7755, 8692, 12293* (all MO); *Foster 735, 961, 1129* (all DUKE); *Shattuck 61, 741* (both F, MO); *Wetmore & Abbe 93, 214* (both F, MO); *Wilson 7* (F, MO); *Woodworth & Vestal 343, 350, 518, 568, 659* (all F, MO); *Zetek 5531* (F, MO). CHIRIQUÍ: Pinola, *Kirkbride & Duke 863* (NY). COCLÉ: La Mesa, *Allen 2690* (MO). El Valle de Antón, crest of Cerro Pajita, 1,100 m, *Allen 3749* (NY). Slopes of Cerro Pilón, near El Valle, 700–900 m, *Duke 12129* (NY). La Mesa, *Dwyer & Nee 11937* (MO); *Gentry 5646* (MO). Mountains beyond La Pintada, *Hunter & Allen 627* (MO). La Mesa above El Valle de Antón, 1,000 m, *Weaver 1654* (DUKE). Bismark above Penonomé, 2,000–3,000 ft, *Williams 559* (NY). COLÓN: Portobelo, *Billberg 231* (S). Santa Rita Trail, *Cowell 128* (NY). Río Miguel de la Borda near Guasimo, *Croat 9914* (MO, NY). Santa Rita Ridge, *Croat 13865* (MO). E Santa Rita Ridge, *Correa & Dressler 633* (MO). Santa Rita Ridge Road, *Mori & Kalunki 2106* (MO). Portobelo, *Pittier 2437* (BM). Ca. 8 km NE of Santa Rita, ca. 650 ft, *Wilbur & Weaver 10852* (DUKE). DARIÉN: Headwater of Río Tuquesa, *Croat 27157* (MO). Without other locality, *MacBride 2707* (F). PANAMÁ: Hills above Campana, 600–800 m, *Allen 1692* (F, MO, NY). Cerro Campana beyond Su Lin Hotel, *Croat 14224* (MO). El Llano-Cartí Road, 12 km from Panamerican Highway, *D'Arcy 10601* (BM, MO). Panamá Viejo, *Duke 5737* (MO). Cerro Campana, *Duke 10755* (MO). Cerro Azul, *Dwyer 1497, 1512, 2642, 3076* (all MO). Goofy Lake to 1.5 mi S, *Dwyer & Hayden 8028* (MO, NY). Cerro Jefe, *Foster & Kennedy 1820* (DUKE). Between Río Espave and Río Agua Clara, *Gentry 3762* (BM, MO, NY). Matachin, *Hayes 456* (MO, NY). Near Panama City, *Hayes* (BM, K). Cerro Campana, *Kirkbride & Hayden 307* (MO, NY). 5–10 km NE of Altos de Pacora, *Mori & Kallunki 3334* (MO). Cerro Azul, *Porter et al. 4099* (MO, NY). Panamá, *Seemann 466* (BM, K). Cerro Azul, *Tyson 2084* (MO). Arraiján, *Zetek 5567* (F, MO). SAN BLAS: Canal just N of Mandinga Airport, *Duke 14840* (MO). Mainland opposite Ailigandí River to 2.5 mi inland, *Lewis et al. 159* (MO). VERAGUAS: Valley of Río dos Bocas, 15.6 km NW of Santa Fé, *Croat 27703* (MO). Mouth of Río Concepción, *Lewis et al. 2779* (MO, NY). 7 km W of Santa Fé, *Nee 11202* (MO).

2. **Vismia jefensis** N. Robson.[4] TYPE: Panama, Goofy Lake to Cerro Jefe, *Correa & Dressler 568* (MO, holotype; DUKE, isotype).

Shrub or *tree* to 6 m tall; bark gray, not flaking; sap orange or red; branches densely chocolate-tomentose, grayish in age, with appressed-stellate hairs and scattered stellate or dendroid pairs, glabrescent or not. *Leaves* petiolate; petiole 12–25 mm long, slender, densely appressed chocolate-tomentose, not glabrescent; lamina 6.0–15.5 cm long, 2.5–6.7 cm wide, ovate to ovate-elliptic or lanceolate, the apex gradually long-acuminate, the base rounded to cuneate, not asymmetric, subcoriaceous, dull or sublucent above, green (if glabrous) or rufous to bronze beneath, the main lateral veins 9–12, darkish brown, uniting in submarginal loops, usually without intermediate lateral veins, and with densely reticulate venation

[4] *Vismia jefensis* N. Robson, sp. nov. *V. rufae* Cuatrecasas affinis sed habitu humiliori saepe fruticoso, foliis lanceolatis vel ellipticis haud oblongis plerumque sine venis lateralibus intermediis instructis, floribus maioribus petalis albis vel eburneis haud roseis, differt.

scarcely prominent on both sides, the glandular dots present, usually completely obscured by the indumentum, the stellate hairs dense, rufous to ferrugineous or bronze, appressed, obscuring the epidermis. *Inflorescences* terminal and axillary, many flowered, broadly pyramidal to subcylindric, 4–5-noded, the basal 1–2 nodes with deciduous bract pairs and the lower nodes with reduced leaves subtending axillary accessory branches; rachis and pedicels chocolate-appressed-tomentose, not glabrescent; buds ellipsoid-globose. *Flowers* homostylous; sepals 5–7 mm long, free, the outermost 3.0–3.5 mm wide, elliptic to narrowly oblong, obtuse to acute, the exposed surfaces densely chocolate appressed-tomentose with stellate hairs, the inner margins ciliate, with numerous glandular streaks and lines, spreading in fruit; petals cream to pale yellow, 7.5–9.0 mm long, 3–4 mm wide, 1.3 times as long as the sepals, obovate to oblanceolate, rounded, erect, with numerous thick black glandular lines or streaks and distally a few dots, internally whitish-villous; stamen fascicles free, deciduous, with ca. 30 stamens, whitish-villous, almost as long as the sepals; staminodial fascicles deciduous, ca. 2 mm long, oblong, distally pilose; ovary ca. 2 mm long, ovoid subglobose, eglandular, glabrous, the styles ca. 2 mm short of the sepal apices, the stigmas narrowly capitate. *Fruits* dark purple, globose, 12 mm long, 12 mm wide, glabrous; seeds not seen.

Vismia jefensis is similar to *V. rufa* Cuatrecasas from lowland Colombia, which differs in habit, being a tree 16–30 m tall, leaf shape lanceolate to elliptic, shortly acuminate to apiculate, flower size generally smaller, e.g., sepals 3.5–4.5 mm long, and petal color pink, not cream to pale yellow. It is confined to the Cerro Jefe area of Panama, where it grows in forest from 750 m to the top (900 m).

PANAMÁ: Between Goofy Lake and Cerro Jefe, *Correa & Dressler 470* (MO), *568* (DUKE, MO). Altos de Pacora, 10 mi beyond Goofy Lake, Cerro Jefe, *Croat 14418* (MO). Cerro Jefe, *Duke 9461* (MO). Cerro Azul to Cerro Jefe, *Dwyer 3370* (MO). Cerro Jefe, *Elias & Hayden 1800* (NY). Ridge between Cerro Azul and Cerro Jefe, *Foster 1166* (DUKE). Punta de Cerro Jefe, *Gómez-Pompa et al. 3072* (MO). Cerro Jefe, down slope from summit, *Kirkbride & Crebbs 10* (MO, NY). Cerro Jefe at and within 2 mi of top, ca. 3,000 ft, *Luteyn 13962* (DUKE). Cerro Jefe, *Porter et al. 5071* (MO, NY). E slope of Cerro Jefe, 2,700 ft, *Tyson 3378* (MO). Cerro Jefe, 2,700–3,000 ft, *Tyson et al. 3206* (MO). Top of Cerro Jefe, 3,000 ft, *Tyson et al. 4432* (DUKE, MO). 8 km above Goofy Lake on road to Cerro Jefe, *Weaver 1501* (DUKE). Cerro Jefe between Cerro Azul and La Eneida, *Wilbur 15544* (DUKE). Cerro Jefe ca. 10 mi beyond Cerro Azul, above Tocumen Airport, *Wilbur 19462* (DUKE). Cerro Jefe beyond Cerro Azul, ca. 5.5 mi towards La Eneida, 2,700–3,000 ft, *Wilbur & Teeri 13605* (DUKE). Cerro Jefe NE of Cerro Azul, *Wilbur & Weaver 11088* (DUKE). Cerro Jefe beyond Cerro Azul, between mi 4 and 8, *Wilbur & Weaver 11364* (DUKE).

3. **Vismia latisepala** N. Robson.[5] TYPE: Panama, Goofy Lake toward Cerro Azul, *Dwyer & Stimson 8058* (NY, holotype; GH, MO, UC, US, isotypes, not seen).

V. baccifera subsp. *ferruginea* sensu Ewan, Contr. U.S. Natl. Herb. 35: 336. 1962, pro parte, non *V. ferruginea* Kunth.

Shrub or *tree*, 2–10(–18) m tall; bark gray, flaking; sap red to yellow; branches densely chocolate- to ferrugineous-tomentose, grayish in age, with appressed-

[5] *Vismia latisepala* N. Robson, sp. nov. *V. japurensi* Reichardt sensu lato affinis sed ramulis inflorescentiae axibusque ferrugineo-tomentosis et plus minusve dense pilis dendrodeis longiusculis obtectis differt; a *V. camparaguey* Sprague et Riley foliis infra ferrugineo-tomentosis, floribus parvis, sepalis latioribus, recidit.

stellate hairs and dense erect stellate or dendroid hairs, not glabrescent. *Leaves* petiolate; petiole (15–)20–32 mm long, densely appressed chocolate- to ferrugineous-tomentose, not glabrescent; lamina 10.5–21.0 cm long, 4.5–10.0 cm wide, oblong-ovate or oblong-lanceolate to ovate or lanceolate, the apex acute or obtuse to shortly and abruptly acuminate, the base shallowly cordate to rounded or more rarely broadly cuneate, rarely asymmetric, chartaceous, dull to sublucent above, ferrugineous beneath, the main lateral veins (10–)13–18, dark or reddish brown, joining the midrib at 90°, uniting in submarginal loops, with or without intermediate lateral veins, and with densely reticulate venation slightly prominent on both sides, the glandular dots present, usually obscured by the indumentum, the stellate hairs dense, appressed, ferrugineous to fawn, obscuring the epidermis, and with dense ferrugineous stellate-dendroid hairs. *Inflorescences* terminal and axillary, 30–40-flowered, pyramidal to subcylindric, 3–5-noded, the basal node sometimes with a deciduous bract-pair, with leaves (reduced or not) at the lower nodes often subtending axillary accessory branches; rachis and pedicels ferrugineous to chocolate appressed or spreading tomentose, not glabrescent; buds globose. *Flowers* homostylous; sepals 7–10 mm long, free or united at the base, the outermost 4–7 mm wide, ovate, obtuse to acute, the exposed surfaces densely ferrugineous to chocolate appressed-tomentose with stellate hairs, the inner margins entire, with numerous glandular streaks and lines, erect in fruit; petals white to yellow, 9–13 mm long, 6–10 mm wide, 1.3 times as long as the sepals, broadly obovate to obovate-spatulate, rounded, erect, with or rarely without numerous distal fine continuous black glandular lines and sometimes marginal short streaks, internally whitish-villous; stamen fascicles free, deciduous, with ca. 70 stamens, whitish-villous, as long as the sepals; staminodial fascicles persistent, ca. 2 mm long, oblong, distally pilose; ovary ca. 2.5 mm long, subglobose, eglandular, glabrous, the styles ca. 2 mm short of the sepal apices, proximally gland dotted, the stigmas broadly capitate. *Fruits* 15–20 mm long, 15–20 mm wide, globose, yellowish green (immature) glabrous; seeds dark reddish brown, ca. 2.5 mm long.

Vismia latisepala has frequently been confused with *V. ferruginea* H.B.K. because of its vivid ferrugineous indumentum. The type of the latter species, however, differs from the Panamanian plant in several respects, e.g., the leaves are finely golden-tomentose beneath and cuneate at the base and the finely ferrugineo-tomentose sepals are reflexed in fruit. In fact, it appears to belong to *V. guianensis* (Aubl.) Choisy or is closely related to that species.

The affinities of *V. latisepala*, on the other hand, are with three species which are geographically peripheral to it. It shares the broad sepals and petals with *V. japurensis* Reichardt from the Guyana Highland and Amazon regions, but differs *inter alia* in its longer indumentum on stem and inflorescence; this character also distinguishes it from a closely related element from Colombia and Ecuador, which has narrower sepals and petals, while *V. camparaguey* Sprague & Riley, from Belize, Guatemala and Mexico, has smaller flowers with narrower sepals and no appressed indumentum on the leaves, the epidermis being visible between the dendroid hairs. The element from Colombia and Ecuador was included by Ewan in *Vismia panamensis*, but it may belong to an undescribed species.

Vismia latisepala appears to be confined to Panama and Colombia. In Panama it is quite common, growing in open woodland, woodland margins, clearings, and grasslands from sea level to 1,000 m.

CANAL ZONE: Ancón Hill, *Bartlett & Lasser 16304* (MO). Pipeline Road, end near Gatún Lake, *Croat 4714* (MO). Gaillard Highway, 2 mi NW of Summit Garden, *Croat 14840* (MO). Fort Kobbe, *Duke 3935* (MO). Frijoles, *Ebinger 88* (MO). 3 mi NW of Gamboa on Navy pipeline road, 60 m, *Haines 470* (DUKE, F). Pipeline road out of Gamboa, sea level, *Luteyn 4158* (DUKE). 17 km NW of Gamboa, 60 m, *Nee 11121* (MO). Ancón Hill, *Standley 25154* (MO). 1 mi NE of Fort Clayton, *Stimson 5191* (DUKE, NY). Albrook Air Force Base, *Tyson 1111, 1117* (both MO). Ancón Hill, *Woodson et al. 1330* (MO, NY). BARRO COLORADO ISLAND: *Aviles 953* (F); *Bangham 409* (F); *Croat 4910* (MO), *6110* (F, MO), *6416, 6695, 10736, 11089* (all MO), *12286* (F, MO); *Foster 374, 646, 648* (all DUKE), *649* (MO); *Shattuck 953* (F, MO); *Wetmore & Abbe 69* (F); *Woodson & Schery 975* (MO, NY); *Woodworth & Vestal 336, 342a* (both MO). COCLÉ: La Pintada, 300 m, *Allen 3606* (NY). El Valle, *Dwyer 1814* (MO). Road to El Valle, *Ebinger 1103* (F, MO). Interamerican Highway ca. 1 mi from entrance to El Valle, *Garner 33* (DUKE). 2 mi E of Río Hondo, *Gentry 2920* (MO). W of Río Guias, *Gentry 5840* (MO). 3 mi from Interamerican Highway on westernmost road to Santa Rita, *Haines 568* (DUKE). Between Las Margaritas and El Valle, *Woodson et al. 1291* (MO, NY). COLÓN: Maria Chiquita, E of Río Piedras towards Portobelo, *Dwyer & Kirkbride 7087* (NY). Santa Rita Ridge, ca. 10 km from Transisthmian Highway to end of road, *Porter et al. 4732* (MO, NY). PANAMÁ: Cerro Campana, *Allen 2442* (MO). Pearl Islands, San José, *Anderson 1852* (F). Cerro Campana, *Duke 8652* (MO). San José Island between Bodega Bay and Río Mata Puerco, *Duke 12542* (NY). Cerro Azul, *Dwyer 1512* (F, MO, NY), *4216* (MO). Tocumen airport, *Dwyer 4229* (MO). 2 mi S of Goofy Lake towards Cerro Azul, *Dwyer & Stimson 8058* (MO, NY). Cerro Azul, *Ebinger 404* (F, MO). Woods near Panamá, *Hayes* (BM). Cerro Campana, *Lewis et al. 3145* (MO, NY). Cerro Campana 8.6 mi SW of Campira, ca. 700 m, *Luteyn 1004* (DUKE, F). Cerro Campana, *McDaniel 6813* (DUKE, MO). Bella Vista, *Piper 5391* (NY). Cerro Campana, above Su Lin Motel, *Porter et al. 4201* (MO). Río La Puente road, Calzada Larga, *Quistgaard 42* (DUKE, MO). Road to Cerro Azul, *Rivas de De Hoyos 1* (MO). Carretera de Cerro Azul, *Rodriguez 1* (DUKE). Villa Rosario, near road to Río Perequete, *Saldana 37* (DUKE). Peñon, Las Cumbres, *Sandoval 49* (DUKE, MO). Near Punta Paitilla, *Standley 26283* (MO). Miraflores Lake, Chorrera, *White 177* (F, MO). Road to Cerro Jefe, shore of Goofy Lake, *Witherspoon & Witherspoon 8442* (BM, MO). Cerro Campana, near Su Lin Motor Lodge, 3,000 ft, *Woods & Woods* (DUKE, MO). Las Sabanas, collector unknown (MO). SAN BLAS: Río Ailigandí, *Duke 10843* (NY). Ailigandí, *Dwyer 6823* (MO). Mainland opposite Achituppu, *Lewis et al. 135* (MO). VERAGUAS: La Yeguada, 560–600 m, *McDaniel & Cooke 14738* (MO). Without other locality, *Hancock* (K).

4. **Vismia macrophylla** H.B.K., Nov. Gen. Sp. Pl. 5: 184. 1822. TYPE: Venezuela, "crescit in ripa obumbrate Fluminis Nigri et Cassiquiares," *Humboldt & Bonpland* (P).

V. angusta Miq., Linnaea 18: 27. 1844. TYPE: Surinam, "ad Osembo in Para," *Focke 382* (U, not seen).

V. latifolia sensu Reichardt in Mart., Fl. Bras. 12(1): 208. 1878, non *V. latifolia* (Aubl.) Choisy (1821).

Tree or rarely *shrub*, 2–25(–43) m tall; bark grayish-rufous, flaking; sap orange (? to yellow); branches densely to sparsely ferrugineous-tomentose, grayish in age, with appressed-stellate to dendroid hairs, glabrescent. *Leaves* with petiole 10–25 mm long, ferrugineous-tomentose; lamina 10.0–40.0 cm long, 6.0–16.3 cm wide, narrowly oblong to lanceolate or ovate, the apex shortly acuminate to apiculate, the base deeply cordate to almost rounded, coriaceous, lustrous or dull above, greenish beneath, the lateral veins 12–31, red, uniting in submarginal loops, often with 1–2 short intermediate lateral veins, and with conspicuous

reticulate venation beneath, the glandular dots dense, sometimes obscured by the indumentum, the indumentum of dense to sparse stellate to dendroid ferrugineous hairs, especially on the veins, not obscuring the finely papillose epidermis. *Inflorescences* terminal, many flowered, pyramidal, 5–6(–7)-noded, with reduced leaves at the lowermost 1(2) nodes, without axillary accessory branches; rachis and pedicels shortly to floccosely ferrugineous to dark brown tomentose, glabrescent or not; buds cylindric to obovoid. *Flowers* heterostylous; sepals 5–6 mm long, free to near the base, the outermost ca. 3 mm wide, oblong or elliptic-oblong, rounded, the exposed surfaces densely whitish-papillose, densely to sparsely ferrugineous- to dark-brown-pubescent with stellate-dendroid hairs, the inner margins fimbriate, with broad glandular lines or streaks and submarginal dots, erect in fruit; petals white or greenish white to cream, 10–13 mm long, 2.0–2.5 mm wide, ca. 2 times as long as the sepals, narrowly oblong-lanceolate, recurved near the apex, distally glandular-punctate, internally whitish-villous; stamen fascicles free, persistent, with ca. 25 stamens, proximally whitish-villous, as long as the sepals (dolichostyly) or petals (brachystyly); staminodial fascicles persistent, ca. 2 mm long, liguliform, distally pilose; ovary ca. 2.5 mm long, pentagonal-subglobose, distally glandular-punctate, glabrous, with the styles equaling the sepals (brachystyly) or petals (dolichostyly), the stigmas broadly capitate to recurved-bifid. *Fruits* green to olive brown or reddish, 12–14 mm long, 11–13 mm wide, broadly ovoid-subglobose to globose, glabrous; seeds dark reddish brown, 2.5–3.5 mm long.

Vismia macrophylla is widespread in northern South America from central Brazil (Bahia, Matto Grosso) and Amazonian Peru northwards; and it also occurs in Costa Rica and northward as far as Mexico (?). It grows in forests, thickets, roadsides and river margins up to 800 m or occasionally higher (to 2,000 m in Colombia). The persistent stamen fascicles distinguish it from all other Panamanian species of *Vismia*. The two forms of flower are particularly noticeable because the stamens or styles protrude beyond the recurved apices of the petals. According to *Duke 8458*, the sap is used by the Cuna Indians to paint or treat blanched places in the skin.

Although forms typical of *V. macrophylla* (i.e., with broad thinner leaves and sparser stellate-dendroid hairs) are commoner in dense forest, and those typical of *V. angusta* (i.e., with narrower thicker leaves and denser stellate-dendroid hairs) are more frequent in more open habitats, the correlation of these characters is not complete and there is no apparent break in the variation to allow them to be recognized, even as varieties.

BOCAS DEL TORO: 4–6 mi N of Almirante, *McDaniel 5099* (MO). Chiriquí Lagoon, Fish Creek Hills, *Wedel 2432* (MO). CANAL ZONE: Gatún Lake, *Bangham 442* (F). Near crossing of Cruces Trail and Madden Dam Road, *Bartlett & Lasser 16341* (MO). T.T.C.—Albrook Tower, *Blum 567* (MO). Pipeline road near Gamboa, *Clewell & Tyson 3313* (MO). Pipeline road, 3 mi N of Gamboa gate, *Croat 15096* (DUKE, F, MO, NY). Between Fort Sherman and Fort Lorenzo, *Croat 15434* (MO). Pipeline road 7 mi N of Gamboa gate, *Croat 16599* (MO). Near Coco Solo weather station, *Duke 4278* (MO). Coco Solo near U.S. Army Tropic Test Center, *Elias & Kirkbride 1608* (NY). Chagres, *Fendler 8* (BM, F, K, MO, US). Pipeline road 3 mi N of Gamboa gate, 60 m, *Haines 469* (DUKE, F, MO). Between Piña and Gatún, *Luteyn 1302* (DUKE, F). Ancón Hospital grounds, 20–80 m, *Pittier 2735* (BM, NY). Agua Clara on the Trinidad River, 10–40 m, *Pittier 3989* (NY). Santa Rita hills, *Smith & Smith*

3424 (F). 6 mi N of Gamboa on ridge S of Río Frijol, *Tyson 1523* (MO). Albrook Air Force Base on Beacon Hill, *Tyson 2039* (MO). BARRO COLORADO ISLAND: *Aviles 112, 893* (both F); *Chickering 37* (F); *Correa & Haines 144* (DUKE); *Croat 5211* (MO), *5322, 6430* (F, MO, NY), *6434* (MO), *6570* (F, MO, NY), *11087* (MO); *Foster 1083, 1914* (both DUKE, F); *Shattuck 893* (MO); *Starry 141* (F, MO); *Woodson & Schery 974* (MO, NY); *Woodworth & Vestal 427* (F, MO). CHIRIQUÍ: Punta Burica, *Lezcano 40* (F, MO). COCLÉ: La Mesa, 5 mi N of El Valle, 2,500 ft, *Tyson et al. 2447* (NY). COLÓN: Miguel de la Borda, *Croat 10039* (F, MO). Between Salud and Boca del Río Indio, Icacal, *Howell 47* (MO). Salud, 50 m, *Lao & Holdridge 183* (DUKE, MO). Santa Rita Ridge road, 8.5 km from Boyd-Roosevelt Highway, *Mori & Kallunki 2113* (MO). Santa Rita road, 1 mi from Carretera Transisthmica, *Stimson 5252* (DUKE, F, NY). DARIÉN: Gold mine at Caná, 500–600 m, *Croat 37625* (BM, MO). La Palma, 0–50 m, *Pittier 5481* (NY). Caná, *Stern et al. 517* (MO, NY). PANAMÁ: Hills above Campana, 600–800 m, *Allen 1304* (MO). SE part of Gatún Lake, vic. of Río Pescado, *Bartlett & Lasser 16597* (MO). Panamá Viejo, *Duke 5738* (MO). Cerro Campana beyond Su Lin Motel, 2,700–3,000 ft, *Duke 8651* (MO). Cerro Azul, *Dwyer 1393* (BM, F, MO), *1532* (F, MO, NY). Cerro Campana above Su Lin Motel, 3,000 ft, *Dwyer & Kirkbride 7862* (MO, NY). Cerro Azul, near Goofy Lake, *Ebinger 977* (F, MO). Calzada Larga, *Fernández 109* (MO). Lago Cerro Azul on way to Cerro Jefe, 800 m, *Nee 11471* (MO). Taboga Island, *Pittier 3593* (NY). Goofy Lake to Cerro Jefe, 8 km, *Weaver & Foster 1487, 1505* (both DUKE). Miraflores Lake, Chorrera, *White 176* (F, MO). Near Arraiján, 15 m, *Woodson et al. 1342* (MO, NY). SAN BLAS: Permé, *Cooper 659* (F, NY). Mulatuppu (Río Ibedí), *Duke 8458* (MO). Inland from Mandinga airport, *Duke 8919* (MO). Isla Pino, near Mulatupo, to ca. 200 ft, *Elias 1720* (MO). VERAGUAS: Río Primero Braso, 2.5 km beyond Agriculture School Alto Piedra, 700–750 m, *Croat 25525* (MO). Mouth of Río Concepción, *Lewis et al. 2777* (MO). NW of Santa Fé, 11 km from Escuela Agricola de Piedra, 450–550 m, *Mori & Kallunki 6139* (DUKE).

5. **Vismia panamensis** Duchass. & Walp., Linnaea 23: 748. 1850. TYPE: Panama, *Duchassaing* (GOET).

Shrub or *tree* to 15(–22) m tall; bark grayish brown, reticulate; sap orange; branches densely to sparsely chocolate- to ferrugineous-tomentose, grayish in age, with appressed-stellate hairs and scattered erect stellate or dendroid hairs, subglabrescent. *Leaves* petiolate; petiole 10–20(–23) mm long, densely appressed ferrugineous-tomentose, subglabrescent; lamina 9.0–26.5 cm long, 3.0–11.0 cm wide, oblong to broadly ovate or lanceolate, often triangular, the apex shortly and gradually acuminate, the base shallowly cordate or truncate to broadly cuneate or shortly narrowed, occasionally asymmetric, chartaceous, dull dark green above, ferrugineous beneath when young, fawn or rarely greenish when mature, the main lateral veins 10–15, dark brown or concolorous, joining the midrib at an obtuse or acute angle (except the very basal ones), uniting in submarginal loops, with or without intermediate lateral veins, the densely reticulate venation slightly prominent on both sides, the glandular dots present, usually obscured by the indumentum, the stellate hairs usually dense, appressed, ferrugineous to fawn, eventually whitish, usually obscuring the epidermis, the stellate-dendroid hairs sparse, ferrugineous. *Inflorescences* terminal and occasionally axillary, 9–many-flowered, pyramidal to subcylindric, 3–5-noded, without deciduous bract pairs, the reduced leaves at the lower node often subtending axillary accessory branches; rachis and pedicels ferrugineous to chocolate appressed pubescent, whitish in age, with scattered spreading stellate to dendroid hairs, not glabrescent; buds globose; pedicels 1.5–2.5 mm long. *Flowers* heterostylous; sepals 5–8 mm long, free, the outermost (2.5–)3.0–3.5 mm wide, oblong to lanceolate, acute, the exposed surfaces densely yellowish-fawn to ferrugineous-

tomentose with appressed stellate hairs, sometimes also with numerous spreading stellate hairs, the inner margins ciliate towards the apex, with numerous glandular lines, spreading to subreflexed in fruit; petals yellow, 7–10 mm long, 3–6 mm wide, 1.2–1.3 times as long as the sepals, obovate-oblanceolate, unguiculate, rounded, erect, with numerous distal thin or thick, continuous or interrupted black glandular lines and sometimes streaks and dots, internally whitish-villous; stamen fascicles free, deciduous, with 40–50 stamens, whitish-villous, exceeding the sepals (brachystyly) or shorter than them (dolichostyly); staminodial fascicles eventually deciduous, 1.5–2.0 mm long, oblong, distally pilose; ovary 2.5–3.0 mm long, broadly ovoid-pentagonal, glandular-punctate and -striate, the styles shorter than the sepals (brachystyly) or exceeding them (dolichostyly), proximally gland dotted, the stigmas broadly capitate. *Fruits* broadly ovoid, 9–14 mm long, 7–12 mm wide, green to black, glabrous; seeds dark brown, ca. 2.2 mm long.

Vismia panamensis is related to *V. latifolia* (Aubl.) Choisy (from Surinam and Cayenne) and *V. guianensis* (Aubl.) Choisy (from Venezuela to eastern Brazil), differing from the former by its smaller, usually narrower leaves and globose (not cylindric) flower buds, from the latter by its shorter pedicels and larger leaves, and from both by its gland-lined petals. It may be confined to Panama, Costa Rica, and Nicaragua, as the specimens from lowland Colombia and Ecuador that Ewan included in *V. panamensis* are more similar to *V. latisepala* N. Robson and probably belong to an undescribed species. In Panama, *V. panamensis* is common in forest clearings, secondary forest, thickets, and scrub from sea level to 1,140 m.

BOCAS DEL TORO: Chiriquicito to 5 mi S along Río Guarumo, *Lewis et al. 2018* (MO, NY). CANAL ZONE: Near Frijoles, 60 m, *Allen 916* (DUKE, F, MO, NY). Pipeline road near Gamboa, *Clewell & Tyson 3259* (MO). Without other locality, *Crawford 439* (NY). Pipeline road near Gatún Lake, *Croat 4718* (MO). Pipeline road, 2.5 mi from Gamboa gate, *Croat 9380* (MO). Gaillard Highway, 2 mi NW of Summit Garden, *Croat 14047* (MO). Road K-10, 1–2 mi from Kobbe Arrayan Highway, *Duke 11715* (NY). Canal Zone, *Eppelsheimer 3* (F). Chagres, *Fendler 7* (BM, K, MO). Gatún, *Hayes 451, 921* (both NY). 5 mi N of Gamboa on Pipeline road, *Lazor 5257* (MO). NW shore of Gatún Lake, *Lewis et al. 1820* (MO, NY). Near Fort Randolph, *Maxon & Harvey 6519* (BM). Navy Reservation, N of Gamboa, *Robyns 65-42* (MO). Chagres, *Seemann 555* (BM, K). Naval Ammunition Depot, *Stern & Chambers 36* (MO). Río Cocolí Road K-9, *Stern et al. 320* (MO, NY). Fort Sherman Research Forest Site off Road 5-2, *Stimson 5097* (NY). Miraflores Lock area, *Tyson 1130* (MO). Near mouth of Río Cocolí, *White 97* (MO). BARRO COLORADO ISLAND: *Bailey 252* (F); *Croat 4614, 4619, 4956, 5523, 5636* (all MO), *8664* (MO, NY); *Ebinger 86* (MO); *Foster 648, 649* (both DUKE); *Shattuck 244* (MO); *Wilbur & Weaver 10788* (DUKE); *Wilson 92* (MO); *Woodworth & Vestal 342, 697, 714* (all MO). CHIRIQUÍ: Boqueté, 3,800 ft, *Davidson 695* (F, MO), *816* (MO). Near Pinola, *Kirkbride & Duke 863* (MO, NY). 1 mi S of Volcán, *Lazor & Correa 2768* (MO). 8 km N of Camp El Volcán, 6,000 ft, *Little 6052* (MO). 17 km NE of San Felix, 1,000 m, *Nee 10667* (MO). Around Caldera, 200–300 m, *Pittier 3360* (NY). 1 mi E of Cuesta del Piedra, 2,800 ft, *Tyson 903* (FSU, MO). COCLÉ: El Valle de Antón, crest of Cerro Pajita, 1,100 m, *Allen 3749* (NY). La Pintada, *de Leon 23* (F, MO). COLÓN: Buena Vista, 100 m, *Holdridge 6386* (DUKE). Icacal, Punta Pedro sawmill, *Howell 77* (MO). DARIÉN: Caná, 1,750 ft, *Stern et al. 543* (MO, NY). HERRERA: 12.5 mi S of Ocú, 1,200 ft, *Lewis et al. 1654* (MO, NY). LOS SANTOS: Bahia Honda, *Barclay 2829* (BM, MO). Loma Prieta, Cerro Grande, 2,400–2,800 ft, *Lewis et al. 2203* (MO, NY). PANAMÁ: Between Gorgona and Cruces, *Barclay 1013* (BM, K). Cerro Azul, *Gómez-Pompa et al. 3421* (MO). Perlas Archipelago, San José Island, *Johnston 19* (BM, MO). Chilibre, *Moseley 21* (F, MO). Chepo, sabana de Juan Corso, 60–80 m, *Pittier 4645* (US). Cerro Azul, 2,000 ft, *Tyson 2177* (MO). E slope of Cerro Jefe, 2,700–3,100 ft, *Tyson 3538* (MO). Perlas Archipelago, Isla Espiritu Santo, *Tyson 5571* (MO). Between Monte Oscuro and Cermeno, *Varela 13* (MO). Cerro Jefe between Cerro Azul and

La Eneida, *Wilbur 15558* (DUKE). Arraiján, *Zetek 5570* (MO). VERAGUAS: Along quebrada just S of Santa Fé, 450 m, *Nee 8050* (MO). 9 mi W of bridge over Río Cobre, Cerro San Cristobal, *Nee 10157* (MO). Between San Francisco and Santa Fé, *Stern et al. 1916* (MO). Canzanas, *Tyson 3609* (MO).

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FLORA OF PANAMA[1]

Part VIII

Family 149. ERICACEAE[3]

BY Robert L. Wilbur[2] and James L. Luteyn[3]

Trees, shrubs, woody vines or herbs (the latter occasionally fleshy mycoparasites although often allegedly saprophytic). *Leaves* alternate but rarely opposite or whorled, simple, estipulate, coriaceous and persistent to membranous and deciduous; leaf scars usually with a single vascular bundle scar, nodes usually with one trace and one gap. Inflorescences basically racemose (either racemes, panicles, corymbs or flowers solitary); pedicels bibracteolate, subtended by a deciduous or persistent bract. *Flowers* mostly bisexual but rarely functionally unisexual (more rarely plants dioecious), actinomorphic or slightly zygomorphic; mostly (4–)5(–7)-parted, typically obdiplostemonous, hypogynous or epigynous and with a typically biseriate perianth; sepals occasionally distinct or more typically calyx 4–5(–7)-lobed, often persistent, valvate, imbricate or reduplicate in bud; corolla occasionally distinct but more typically of 4–5(–7) united petals, commonly funnelform, campanulate or urceolate, and valvate, convolute or imbricate in bud; stamens usually twice as many as the petals (or rarely just as many), borne on the edge of a nectariferous disc or rarely epipetalous, distinct or united, the anthers 2-celled, apparently inverting during development, dehiscing longitudinally or more typically by apical clefts or pores, often with distinct or connate tubules and often with terminal awns or abaxial spurs, pollen grains in tetrads or less frequently single (Monotropoideae); pistil (2)4–5(10)-carpellate; stigma simple but occasionally weakly lobed, the style single, the ovary 1, superior or inferior, usually with as many locules as carpels or with twice as many locules as carpels or rarely loculate in lower portion and 1-locular above the placentation axile, the ovules numerous or rarely solitary, anatropous to campylotropous with a single integumentary layer. *Fruit* a loculicidal or septicidal capsule, berry or drupe with a usually persistent, rarely accrescent and fleshy calyx; seeds usually small, anatropous, rarely winged or tailed.

The Ericaceae is a family of about 100 genera and perhaps 3,000 species,

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[1] Grateful acknowledgment is made to the Duke University Research Council and especially to the National Science Foundation (GB-13815 and DEB-76-10185) for their support which made this study feasible. Our thanks should also be expressed to the curators of the herbaria listed below whose willingness to loan specimens, often for an extended period, made this study possible: A, CR, DUKE, F, FSU, GH, M, MO, NY, PMA, SCZ, US, WIS. Study and publication were assisted by National Science Foundation Grant DEB77-04300 (W. C. D'Arcy, principal investigator).

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Ann. Missouri Bot. Gard. 65: 27–144. 1978.

0026-6493/78/0027–0144/$11.95/0

widely distributed in the temperate regions of both hemispheres and in the tropics where it is more abundant in the mountains.

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KEY TO THE GENERA

a. Leaves whitish, pinkish or reddish or at least not green (i.e. lacking chlorophyll); plants herbaceous, succulent ..... 12. *Monotropa*

aa. Leaves green; plants woody shrubs or trees.

b. Petals distinct; fruit a 6–7 locular, septicidally dehiscent capsule ..... 4. *Befaria*

bb. Petals united; fruit a berry, drupe or if a capsule, then loculicidal.

c. Ovary superior.

d. Anther sacs (thecae) each terminated by 2, ascendent to erect awns; calyx lobes either closely appressed to base of fruit or becoming somewhat succulent and accressant at maturity; fruit a berry or capsule, many seeded, with a smooth or pubescent surface but never beset with columnar projections.

e. Calyx neither becoming succulent in fruit nor enveloping the berry, calyx lobes in fruit less than ¼ length of the berry; flowers solitary in the axils of the upper leaves ..... 13. *Pernettya*

ee. Calyx becoming somewhat succulent in fruit accrescent, and closely enveloping the basal ⅔ of the capsule; calyx lobes in fruit more than ½ the length of the capsule; flowers in terminal or axillary racemes or panicles ..... 8. *Gaultheria*

dd. Anther sacs (thecae) each bearing a single reflexed or dorsally spreading awn; calyx lobes never becoming fleshy and either spreading or reflexed; fruit a drupe with 4–10, seed-like nutlets and with the surface always densely beset with columnar projections ..... 3. *Arctostaphylos*

cc. Ovary inferior.

f. Hypanthium continuous with the pedicel, the pedicel not jointed.

g. Hypanthium winged or angled.

h. Flowers solitary; corolla 1 cm long or less; pedicels shorter than the flowers, less than 3 mm long, bibracteolate; stamens less than 5 mm long; coralla unwinged ..... 17. *Themistoclesia*

hh. Flowers in 2–4-flowered racemes; corolla 1.5 cm long or more; pedicels as long as the flowers, ca. 15 mm long or longer, ebracteolate; stamens ca. 10 mm long; corolla 5-winged ..... 2. *Anthopterus*

gg. Hypanthium wingless.

i. Flowers and fruits borne on slender, elongate pedicels equalling or longer than the subtending leaves.

j. Calyx 10 mm or longer; corolla 20 mm long or longer; stamens 10 mm long or longer ..... 6. *Didonica*

jj. Calyx 4 mm long or less; corolla 6(–12) mm long or less; stamens 5(–9) mm long or less ---- 16. *Sphyrospermum*

ii. Flowers and fruits borne on pedicels much shorter than the subtending leaves ---------- 19. *Vaccinium*

ff. Hypanthium disarticulating from the pedicel, the pedicel clearly jointed just below the flower.

k. Calyx basally clasped by 2, ovate, pedicellary bractlets so as to be largely hidden from view; pedicels less than 2 mm long ---------- 7. *Disterigma*

kk. Calyx not basally clasped by 2, ovate, pedicellary bractlets and not largely hidden by them; pedicels mostly more than 2 mm long.

l. Anthers dehiscing by longitudinal slits extending for much of the length of the anther sacs; tubules rudimentary, less than 0.4 mm long ---------- 9. *Lateropora*

ll. Anthers dehiscing by pores or clefts on the tubules, these not extending onto the anther sacs; tubules well developed, 1 mm long or longer.

m. Stamens with filaments and anthers all of the same length.

n. Anther sacs rigid and coarsely granular; tubules rigid.

o. Anther connectives unspurred; tubules united completely with a single passage or laterally connate but with 2 passages or rarely distinct to their bases ---------- 11. *Macleania*

oo. Anther connectives all or alternately laterally spurred; tubules distinct to their bases ---------- 14. *Psammisia*

nn. Anther sacs flexible and smooth or finely granular; tubules flexible.

p. Anthers spurless.

q. Inflorescence paniculate; filaments connate; corolla white or pinkish ---------- 18. *Thibaudia*

qq. Inflorescence corymbose; filaments distinct; corolla greenish or greenish yellow ---------- 19. *Vaccinium*

pp. Anthers dorsally spurred.

r. Leaves 5-plinerved, entire; hypanthium conspicuously 5-winged ---------- 1. *Anthopteropsis*

rr. Leaves pinnately veined, serrulate; hypanthium wingless ---------- 19. *Vaccinium*

mm. Stamens, filaments or anthers or both alternately unequal, obviously of 2 lengths.

s. Filaments clearly unequal in length, distinct or rarely weakly coherent at the very base.

t. Calyx lobes 5, less than 1 cm long; anthers alternately unequal in length; stamens more than half as long as the corolla, floral bracts usually longer than 10 mm and always at least 3 mm long ---------- 5. *Cavendishia*

tt. Calyx lobes 3, 1.5 cm long or longer; anthers equal in length; stamens about ⅓ as long as the corolla; floral bracts ca. 1.5 mm long ---------- 10. *Lysiclesia*

ss. Filaments of equal length, connate for their entire length ---------- 15. *Satyria*

1. ANTHOPTEROPSIS

Anthopteropsis A.C. Smith, Ann. Missouri Bot. Gard. 28: 441. 1941. TYPE: *A. insignis* A.C. Smith.

Epiphytic *shrubs*. *Leaves* short petiolate, subcoriaceous, plinerved, entire. *Inflorescences* terminal or rarely axillary, racemose, with the 5–12 flowers borne on medially bibracteolate pedicels subtended by a minute papery bract and articulated with the hypanthium. *Flowers* with the hypanthium fleshy, subglobose, conspicuously and broadly 5-winged to the sinuses, calyx limb erect, the lobes 5, inconspicuous, toothlike and minutely apiculate; corolla tube fleshy, cylindric, inconspicuously 5-angled, the lobes small, deltoid; stamens 10, equal, about half as long as the corolla, the filaments distinct, membranaceous, the anthers inserted dorsally near the base, the thecae slightly to coarsely granular, basally short appendaged, the connectives alternately medially and dorsally spurred, the tubules flexible, dehiscent over their entire length by elongate clefts; style filiform, equalling or slightly exceeding the corolla tube, the ovary inferior, 5-loculate, crowned with an annular disc. *Fruit* a berry.

Anthopteropsis is a monotypic genus endemic to central Panama. It is allied to *Macleania* and especially to *Psammisia*. Its alternately and inconspicuously spurred anthers are similar to those of some South American species of *Psammisia*. Additional collections and further study might suggest its inclusion in *Psammisia*.

1. **Anthopteropsis insignis** A.C. Smith, Ann. Missouri Bot. Gard. 28: 441. 1941. TYPE: Panama; Coclé, El Valle de Antón, *Allen 2500* (A, holotype; MO, isotype).—FIG. 1.

Epiphytic *shrub* to 4 m tall, mature branches terete, glabrous; bark grayish when dry, cracking longitudinally; immature branches and twigs of new growth subterete or bluntly angled, somewhat striate, puberulous, yellowish or reddish brown when dry. *Leaves* coriaceous, elliptic to oblong elliptic, (3–)4.5–6 cm long, (1.5–)2–3 cm wide, basally rounded, narrowly rounded or subcordate, apically subacute, rounded, obtuse or bluntly short acuminate, glabrous except puberulous along the nerves above; 3(–5)-plinerved, the midrib, the lateral nerves and the veinlets reticulate, all raised slightly on both the surfaces; petioles subterete, slightly flattened above, puberulous, 2–3 mm long and 2 mm in diameter. *Inflorescence* 5–8(–12)-flowered; rachis coarsely angled, striate, glabrous, 2–13 mm long; floral bracts ovate to deltoid, acuminate to subacute, ca. 1.5 mm long, ca. 2 mm wide, marginally glandular fimbriate; pedicels subterete, rugulose, swollen distally, 10–20 mm long, 1–2 mm in diameter, inconspicuously puberulous and with scattered glandular fimbriae distally; bracteoles ovate to deltoid, acuminate to subacute, ca. 1–1.5 mm long, 1 mm wide, marginally glandular fimbriate, located at the middle of the pedicel. *Flowers* with the hypanthium fleshy, glabrous, bright pink to red, (5.5–)6–9 mm long, 8–10 mm in diameter including wings, the tube 4–5 mm long, the limb 3–4 mm long, the lobes apiculate, the wings 1.5–2(–3) mm broad and conspicuously veined, corolla cylindric, angled but not winged, yellow, glabrous but often with scattered glandular fimbriae, (16.5–)17–19 mm long, 3–4 mm in diameter, the lobes 1.0–2.0 mm long, 2.0–2.5 mm wide, flaring at anthesis; stamens 9–10.5 mm long, the filaments distinct but often adnate to base of the corolla tube, 2.0–3.0 mm long, 1.3 mm wide

FIGURE 1. *Anthopteropsis insignis* A. C. Smith.—A. Habit (×7/10).—B. Flower (×7/8). [After *Allen 2946* (MO).]

at the base, marginally pilose distally and onto the connective, the anthers 7–9 mm long, the thecae 4.0–5.5 mm long, with a short, caudate, occasionally pubescent, basal appendage, the tubules flexible, acute, slightly narrower than the thecae, dehiscent over the entire length; style exserted, 18–20 mm long. *Berry* red, 7–9 mm long.

COCLÉ: Hills S of El Valle de Antón, 700 m, *Allen 2500* (A, MO). Region S of El Valle de Antón, 700 m, *Allen 2946* (A, F, GH, MO, NY, US). Hills N of El Valle de Antón, *Allen 3556* (F, GH, MO, NY, US). PANAMÁ: Cerro Jefe 700 m, *Dressler 3680* (DUKE, PMA). Road past Cerro Azul, 20 km from Interamerican Highway, *Mori & Kallunki 2212* (MO). El Llano-Cartí Road, 9 km from Interamerican Highway, 350 m, *Mori & Kallunki 5157* (MO).

2. ANTHOPTERUS

Anthopterus Hook., Icon. Pl. 3: *pl. 243.* 1840. TYPE: *A. racemosus* Hook.

Low *shrubs* or small *trees*. *Leaves* alternate but occasionally appearing subopposite, petiolate, coriaceous, plinerved or pinnatinerved, entire. *Inflorescence* axillary, racemose, with several to many flowers; floral bracts solitary at base of pedicel, to 20 mm long but usually small and inconspicuous; pedicels either naked or more typically bibracteolate, continuous with the flower. *Flowers* with the hypanthium prismatic, broadening distally and winged opposite the sinuses; calyx limb suberect, the lobes 5, lanceolate triangular; corolla subcylindric, cylindric urceolate or subglobose, broadly 5-winged opposite the lobes, the lobes triangular, subacute; stamens 10, equal, nearly as long as the corolla, the filaments equal, membranous, distinct or basally slightly connate or connate for half their length, the anthers dorsifixed, membranous with smooth thecae, the tubules usually longer than the anther sacs and opening by short to elongate, introrse clefts; ovary inferior, the stigma truncate, the style filiform, about as long as the corolla, basally surrounded by an annular or cupuliform disc. *Fruit* a berry with numerous small seeds.

Anthopterus is a genus of about five species ranging from eastern Panama to northeastern Peru. There are few collections of any of the species and hence the range of variation within the genus is unknown. *Anthopterus* is closely related to *Thibaudia* and is traditionally separated from that genus by the conspicuously winged calyx and corolla of the former genus in contrast to the wingless or merely angulate calyx and corolla of *Thibaudia*.

1. **Anthopterus wardii** Ball, Hook. Icon. Pl. 15: *pl. 1465.* 1884. TYPE: Colombia: Dept. of El Valle: Buenaventura, near sea level, *Ward s.n.* (K, holotype, not seen).—FIG. 2.

Thibaudia wardii (Ball) Hoerold, Bot. Jahrb. Syst. 42: 274. 1909.

Epiphytic *shrub* or low *tree*; mature branches terete, glabrate; immature branches and twigs of new growth terete, puberulous, tan when dry. *Leaves* oblong or ovate oblong to lance elliptic, 6–13 cm long, 2.5–6 cm wide, basally subcordate, bluntly acuminate, puberulous proximally along the midrib above, glabrous elsewhere, entire, the margin slightly revolute, 5–7-plinerved, the secondary veins originating near the base and the midvein flush or slightly impressed

FIGURE 2. *Anthopterus wardii* Ball.—A. Habit (×⅗).—B–C. Stamens.—B. Lateral view (×5).—C. Ventral view (×5). [After *Archer 1901* (NY), Colombia.]

above, prominently elevated beneath, the veinlets copiously reticulate and slightly raised on both the surfaces; petioles subterete, flattened above, puberulent, 3–5 mm long, 1.5–2 mm in diameter. *Inflorescence* axillary, short racemose with usually ca. 4 flowers; rachis subterete basally, 1–2 cm long, basally surrounded by several triangular to oblong bracts 3–5 mm long; pedicels subterete basally but becoming winged distally, striate, glabrous, 10–20 mm long, each subtended by an oblong bract 3–6 mm long with scattered glandular fimbriae; bracteoles lacking. *Flowers* glabrous; hypanthium urceolate to obprismatic, ca. 8–9 mm long, the wings ca. 1–1.5 mm wide, the limb subspreading, 8–9 mm long including the lobes; calyx lobes triangular ovate, acute, 5–7 mm long, 4–5 mm wide at the base, ca. 7 parallel, branching veins not quite extending to the margin; corolla white, membranous when dry, 10–14 mm long, ca. 16 mm in diameter at the widest point, slightly contracted at both the base and apex and with semiobovate wings 2–5 mm wide, a single longitudinal vein parallel to the margin, the lobes ovate, apiculate, ca. 1 mm wide; stamens 8–10 mm long, the filaments ca. 4 mm long, membranous, connate for about ½ their length, adnate to the corolla; anther sacs ca. 2 mm long, gradually tapering into flexible tubules ca. 3 mm long and opening by introrse clefts about ½ the length of the tubule; stigma truncate.

Anthopterus wardii ranges along the Pacific slope of the Western Cordillera of the Andes from eastern Panama (Darién) into Ecuador. It occurs from near sea level to 1,200 m altitude.

DARIÉN: Cerro Pirre, *Bristan 610* (MO); *Bristan 611* (MO). Cloud forest or mossy forest, Cuasí-Caná; trail between Cerro Campaniento and La Escalera to "Paramo" E of Tres Bocas, *Kirkbride 1308* (MO). Crest of the Cañá-Cuasí Trail, 5500 ft, *Terry 1569* (F).

3. ARCTOSTAPHYLOS

Arctostaphylos Adans., Fam. Pl. 2: 165. 1763. nom. conserv. TYPE: *A. uva-ursi* (L.) K.P.J. Sprengel.

Uva-Ursi [Tourn.] Miller, Gard. Dict. abr. ed. 4. 1754.
Comarostaphylis Zucc., Abh. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. 2: 331. 1837. TYPE: *C. arguta* Zucc.
Xerobotrys Nutt., Trans. Am. Philos. Soc. ser. 2. 8: 267. 1843.
Xylococcus Nutt., Trans. Am. Philos. Soc. ser. 2. 8: 258. 1843. TYPE: *X. bicolor* Nutt.
Daphnidostaphylis Klotzsch, Linnaea 24: 79, 87. 1851.
Arctous (A. Gray) Niedenzu, Bot. Jahrb. Syst. 11: 180. 1889. TYPE: *A. alpina* (L.) Niedenzu.
Ornithostaphylos Small, N. Amer. Fl. 29: 101. 1914. TYPE: *O. oppositifolia* (Parry) Small.
Schizococcus Eastw., Leafl. W. Bot. 1: 98. 1934. TYPE: *S. nummularia* (A. Gray) Eastwood.

Shrubs or small *trees* with diffuse to prostrate or erect stems. Leaves persistent or rarely deciduous, usually coriaceous, rarely membranous, often revolute, entire, undulate or toothed, pinnately veined, petiolate or sessile. *Inflorescence* of few to numerous flowers borne in terminal, solitary or clustered, racemelike panicles; pedicels slender, bibracteolate at or near the base, each subtended by a persistent or deciduous bract. *Flowers* with the calyx persistent with (4)5 nearly distinct lobes much longer than the calyx tube, spreading or reflexed at maturity; corolla urceolate, cylindric, ovoid, globular to somewhat campanulate, (4)5-lobed and the lobes often recurved or spreading; stamens (8)10, included, the filaments dilated and usually basally pubescent, the anthers introrse, each

anther sac with a recurved dorsal hornlike spur, the thecae opening by introrse terminal pores; stigma minute or slightly capitately dilated, the style slender to columnar, ovary superior on a hypogynous disc, (2–)4–5(–10) celled. *Drupe* globose, usually fleshy but rarely dry, the pericarp smooth to papillose or warty; nutlets 4–10, seedlike, each with a solitary seed, the nutlets irregularly separable or united into a solid stone.

Arctostaphylos when broadly interpreted is a genus of about 50 species with one species circumboreal and the remainder mostly restricted to western North and Central America. The genus is broadly circumscribed here to include all those members of the tribe Arbuteae with a solitary seed in each locule. The southern Central American representatives all belong to the segregate genus *Comarostaphylis* which is characterized by fleshy drupes with a papillate pericarp surrounding a solid stone of 3–5 locules and a single seed within each compartment. In contrast to the broader generic usage adopted here, *Arctostaphylos* is often restricted to include only those species with a more or less smooth, nonpapillate pericarp.

1. **Arctostaphylos arbutoides** (Lindl.) Hemsl., Biol. Centr. Amer., Bot. 2: 278. 1881.—FIG. 3.

Comarostaphylis arbutoides Lindl., Bot. Reg. 29, *pl. 30*. 1843. TYPE: plants grown in London from seed gathered at Quezaltenango, Guatemala, not seen.
Comarostaphylis chiriquensis Camp, Ann. Missouri Bot. Gard. 26: 297. 1939. TYPE: Panama, Chiriquí, Volcán de Chiriquí, *Woodson et al. 1033* (NY, holotype; MO, NY, isotypes).
Comarostaphylis sleumeri Suessenguth, Bot. Jahrb. Syst. 72: 282. 1942. [as *Comarostylis*]. TYPE: Costa Rica, Chirripó, 3400–3837 m, *Kupper 1319, 1173* (M, syntypes).

Bushy *shrub* or small *tree* 1–4(–5) m tall; young branchlets moderately to densely puberulous, often also sparsely to moderately but inconspicuously glandular pubescent, the pubescence often giving an overall ferrugineous or grayish appearance. *Leaves* coriaceous, elliptic to oblong or oblanceolate, (3–)5–7(–9) cm long, ca. (0.8–)1.0–2.5(–3.0) cm wide, apically acute and tapering basally, while immature moderately flocculent above with ferrugineous, crispy trichomes, glabrous and shiny at maturity, moderately to densely grayish or ferrugineously tomentulose beneath, marginally entire to obscurely undulate, somewhat revolute, the midvein and the primary lateral veins somewhat impressed above and elevated beneath; petioles mostly 4–12 mm long, terete, channeled above, grayish to ferrugineous puberulous but often glabrescent. *Inflorescence* terminal, densely paniculate, the rachis and the inflorescence branches moderately but inconspicuously puberulous, often also with a pilose scattering of gland-tipped, short trichomes; pedicels terete, (1–)1.5–3.0(–5) mm long, densely puberulous, often with gland-tipped, short trichomes subtended by a bract and bracteoles, the bract slightly keeled, deltoid to elliptic, 2.0–3.5 mm long, adaxially glabrous, abaxially puberulous, often sparingly beset with gland-tipped short trichomes, the bracteoles 2, nearly medial, linear to lanceolate, abaxially puberulous, acute, 1.5–2.5 mm long. *Flowers* with the calyx lobes 5, 1.5–2.0 mm long, deltoid to triangularly ovate, acute, adaxially puberulous; corolla urceolate, creamy white or pale yellow, mostly 5–6(–7) mm long, ca. 3.5–4.5 mm in diam., externally

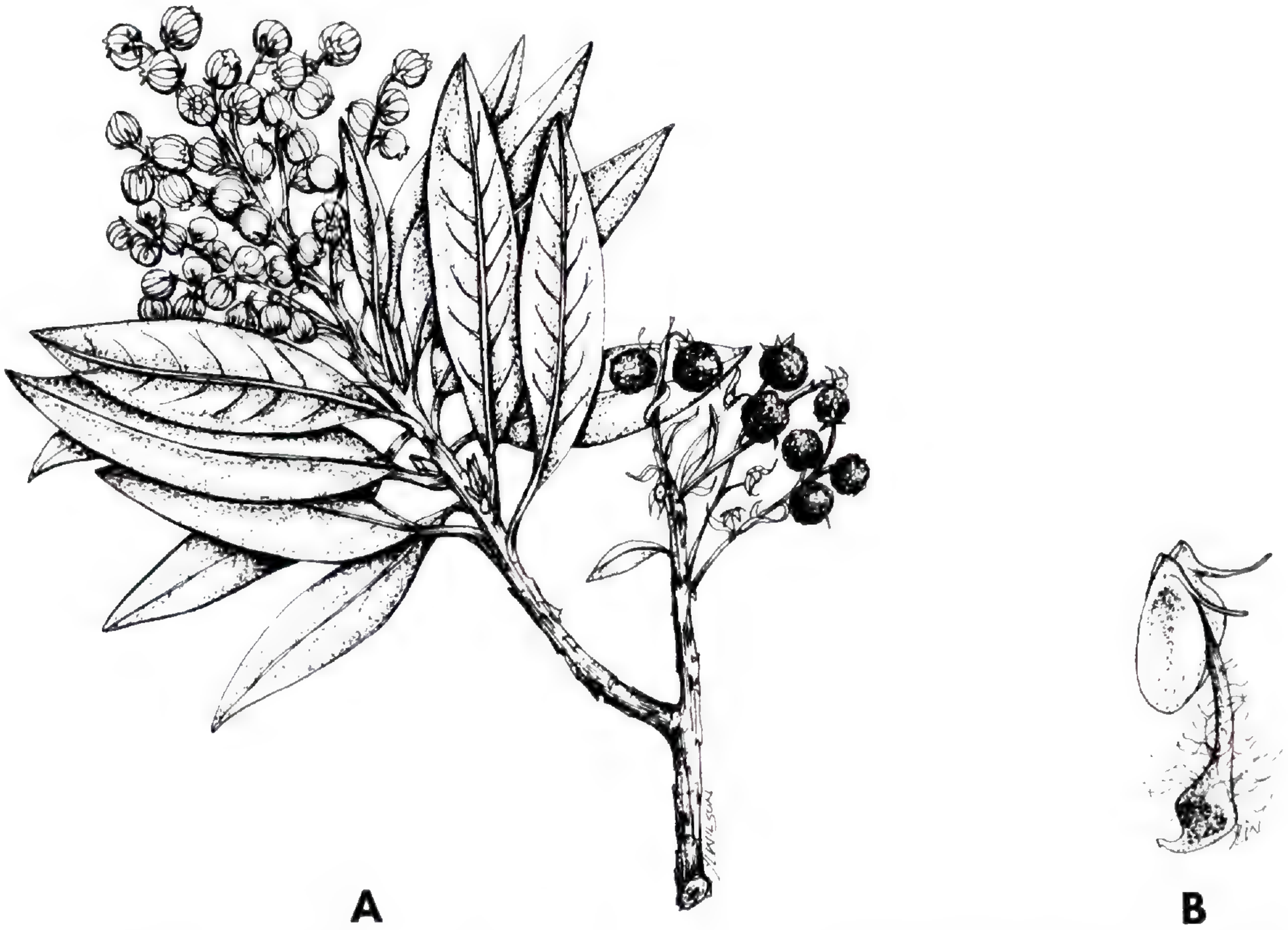


FIGURE 3. *Arctostaphylos arbutoides* (Lindl.) Hemsl.—A. Habit (×3⅗).—B. Stamen, lateral view (×10). [After *Wilbur et al. 15412A* (DUKE).]

glabrous to indistinctly and finely puberulous or pilosulose, the lobes shallowly oblong, apically undulate, 0.5–0.7 mm long, ca. 1.5 mm wide, spreading to recurved; stamens 10, 2.5–3.0 mm long, the filaments arching, basally swollen, pilosulose, the anthers attached medially, 2.0–2.5 mm long, the anther sacs 1.0–1.3 mm long with dorsal spurs ca. 0.5 mm long; stigma slightly broader than the style, style glabrous, 2.5–3.0 mm long, 0.5–0.7 mm in diam., the ovary glabrous or pilosulose, soon glabrate, verruculose. *Drupe* ovoid to globose, glabrous, conspicuously warty, 4–6(–7) mm in diameter.

This is a widespread species, highly variable, especially in the type and distribution of pubescence. The species apparently ranges from southern Mexico southward into Panama. The synonyms listed above are based on minor variations in pubescence and are not worthy of formal taxonomic status. A Costa Rican variant which occurs on Volcán Irazú is recognized as var. *costaricensis*.[4]

The var. *costaricensis* is apparently the only variant occurring on Volcán Irazú. A collection is known from Alajuela Province from Palmira, *Austin Smith P2239* (A). Its range appears to be restricted to the Cordillera Central. The

[4] **Arctostaphylos arbutoides** var. **costaricensis** (Small) Wilbur & Luteyn, comb. nov. *Comarostaphylis costaricensis* Small, N. Amer. Fl. 29: 89. 1914. TYPE: Costa Rica, Prov. de Cartago, Volcán Irazú, *O. Kuntze 2361* (NY). *Arctostaphylos costaricensis* (Small) Standley, Fieldiana, Bot. 4: 320. 1929. Young branchlets glabrous. Leaves glabrous beneath or nearly so. Rachises glabrous to moderately glandular pubescent. Calyx lobes glabrous or merely ciliate.

more widespread typical variety has puberulent branchlets, leaves moderately to densely ferrugineous beneath and densely puberulent calyx lobes. In southern Central America it is found in the Talamanca Range of Costa Rica and Panama.

CHIRIQUÍ: Summit and SW face of Cerro Copete, 9000 ft, *Allen 4888* (MO, US). Llano del Volcán, 1500–1600 m, *Allen & Fairchild 3460* (F, MO, NY, US). Volcán Barú, E slopes along road to summit, 1 mi. from summit, 3000 m, *Croat 34914* (MO). Summit of El Barú, 3225–3447 m, *Croat 34929* (MO). Upper rim of Potrero Muleto, *Croat 34949* (DUKE). Roadside, Potrero Muleto to summit of El Barú, *D'Arcy 10154* (DUKE, MO). Top of peak between Barú and Respinga, ca. 3000 m, *D'Arcy 10096* (DUKE, MO, NY). E slope of Volcán de Chiriquí (Barú), WNW of Boquete, 1900–2000 m, *Davidse & D'Arcy 10166* (DUKE, MO, NY). Elfin forest on ridges above Potrero Muleto, 11 km WNW of Boquete on W slope of Volcán de Chiriquí, *Davidse & D'Arcy 10259* (MO, NY). Lava flow 3 km NE of El Hato del Volcán, *Davidse & D'Arcy 10405* (MO, NY). Volcán de Chiriquí, Boquete District, 7000 ft, *Davidson 906* (A, F, US); 9000 ft, *Davidson 974* (A, F), 11500 ft; *Davidson 1292* (F); 3000 m, *Gutierrez* (PMA); 3600 m, *Killip 3594* (US). Wooded slopes 6.7 mi W of Boquete, 8000 ft, *Luteyn 1489* (DUKE, MO). Moist summit of Cerro de Lino above El Boquete, 1560 m, *Maxon 5210a* (US). W side of Volcán Barú, 2000–2500 m, *Mori & Bolten 7365* (MO); 1500 m, *Mori & Kallunki 5694* (DUKE, MO). Forest of Cerro de Lino, above El Boquete, 1300–1560 m, *Pittier 3038* (US). Volcán de Chiriquí, *Pittier 3095* (F, US); *Sapper s.n.* (US); 11000 ft, *Terry 1292* (A, MO). Potrero Muleto, Volcán de Chiriquí, Boquete, 10400 ft, *Terry 1312* (A, F). Dry windswept canyon bottom, 8 mi NE of El Volcán, 8100–8400 ft, *Tyson 836* (FSU, MO). W slope of El Barú, 6000–7000 ft, *Tyson & Loftin 5956* (FSU); above 11000 ft, *Tyson & Loftin 6156* (FSU, MO). Top of El Barú, *Tyson & Loftin 6166* (FSU, MO). Lava flow NE of El Hato del Volcán near Aguacate, *Wilbur et al. 10964* (DUKE, MO, PMA, US). Old lava field 4 mi NE of El Hato del Volcán near Río Macho del Monte; 1800 m, *Wilbur et al. 13065* (DUKE, MO); 1950 m, *Wilbur et al. 15412A* (DUKE, PMA, US); 6200 ft, *Wilbur et al. 17222* (DUKE). Potrero Muleto to summit of Volcán de Chiriquí, 3500–4000 m, *Woodson & Schery 413* (NY). Loma Larga to summit, Volcán de Chiriquí, 2500–3380 m, *Woodson et al. 1033* (MO, NY).

4. BEFARIA

Befaria Mutis ex L., Mant. 2: 152, 242. 1771. TYPE: *B. aestuans* L.

Acunna Ruiz & Pavón, Fl. Peruv. Chil. Prodr. 69, *pl. 12*. 1794.
Jurgensenia Turczaninov, Bull. Soc. Imp Naturalistes Moscou 20: 151. 1847. TYPE: *J. mexicana* Turcz.

Shrubs or small, slender *trees*, glabrous to densely glandular setose. *Leaves* alternate, petiolate, persistent, entire or rarely obscurely denticulate, the margins flat to tightly revolute. *Inflorescence* terminal or axillary, racemose to corymbose, few to many flowered, often viscid. *Flowers* with the calyx campanulate, (5)7(8)-parted, the lobes persistent; corolla of (5)7(8) distinct, showy petals, these imbricate in bud, the odd petal abaxial, white to pinkish or red, suberect or slightly spreading at anthesis, soon deciduous; stamens twice as many as the petals or more (10–20), about as long as the petals, the filaments free, distinct, elongate, basally dilated and densely pilose, the anthers oblong obconic, dorsifixed, slightly awned, obliquely 2-pored at the apex; stigma capitate, 7-grooved, the style terete, glabrous, elongate and often bent to one side; ovary superior, glabrate, 6–7-locular, the numerous ovules borne on a conspicuous axile placenta. *Capsule* subglobose, septicidally 7-valvate from the apex; many-seeded.

Befaria is a difficult genus of perhaps 25 highly variable species, ranging from Georgia and Florida to Cuba, and from Mexico south into Bolivia. The most re-

cent revision of the genus (Mansfeld & Sleumer, 1935) is unsatisfactory due to the extreme variation encountered in such "key" characters as plant indumentum and corolla size. One species has recently been found in Panama.

Literature:

Camp, W. H. 1941. Studies in the Ericales. A discussion of the genus *Befaria* in North America. Bull. Torrey Bot. Club 68: 100–111.

Mansfeld, R., and H. Sleumer. 1935. Revision der Gattung *Befaria* Mutis. Notizbl. Bot. Gart. Berlin-Dahlem 12: 235–276.

1. **Befaria glauca** Humboldt & Bonpland, Pl. Aeq. 2: 118, *pl. 117*. 1809 [1813]. TYPE: Venezuela, *Bonpland 644* (Herb. Willd. no. *9124*) (P, holotype?; B, isotype, neither seen)—FIG. 4.

Tree 5–6 m tall, mature stems glabrous, terete; bark grayish black, cracking reticulately; immature branches coarsely ribbed, glabrous but becoming densely ferrugineous tomentose at the tips of the new growth. *Leaves* lance elliptic, 2–4.5 cm long, 0.8–1.5 cm wide, basally cuneate and decurrent, apically acute, apiculate, glabrous on both the surfaces when mature, younger leaves weakly ferrugineous tomentose along the midrib on both the surfaces, lamina dark olive green above and pale green beneath when dry; pinnately veined with midrib impressed above and conspicuously raised beneath, veinlets obscure on both the surfaces; petiole 5–10 mm long, glabrate when mature, ferrugineous tomentose when immature, subterete, slightly winged. *Inflorescence* short racemose or subcorymbose, 10–20-flowered; rachis 1.5–2.5 cm long, subterete, coarsely angled, densely ferrugineous tomentose; floral bracts and bracteoles oblong, acute, 2–5 mm long and ca. 1 mm wide, ferrugineous tomentose on both the surfaces; pedicels subterete, striate, 15–24 mm long and ca. 0.5 mm in diameter, densely ferrugineous tomentose becoming glabrate. *Flowers* with the calyx 2–3 mm long, densely ferrugineous tomentose, glabrescent, the lobes 1.5–2 mm long, ovate, obtuse, marginally ciliate; corolla 15–17 mm long, the petals obovate, densely ciliate at distal tips, light pink, with darker pink "honey guides"; stamens 15–16 mm long, the filaments 13–14 mm long, densely pilose on the basal third, the anthers obconic, ca. 2 mm long; style 21–22 mm long, to 28 mm long after anthesis, glabrous; stigma capitate; ovary glabrous. *Capsule* 7–8 mm in diameter.

Befaria glauca is geographically the most widespread and morphologically the most variable species in the genus. Mansfeld & Sleumer (1935) recognized five varieties within the species and these were distinguished primarily by characters of indumentum. This ephemeral character is unusable as its facies change with the age of the plant. Therefore, the varieties of *B. glauca* based on indumentum are questionable. Without personal extensive field experience, we cannot evaluate the problem critically. The Panamanian material seemingly falls within the morphological variability of var. *coarctata* but grades into var. *glauca*.

CHIRIQUÍ: Cerro Colorado, 50 km N of San Félix on the continental divide, cloud forest, 1200–1500 m, *Mori & Dressler 7830* (DUKE, MO), 7833 (DUKE, MO). N of San Félix at

FIGURE 4. *Befaria glauca* Humboldt & Bonpland. Habit (×3/5). [After *Mori & Dressler 7833* (MO).]

Chiriquí-Bocas del Toro border, on Cerro Colorado copper mine road along continental divide, 5000–5500 ft, *Mori & Kallunki 5811* (DUKE, MO). VERAGUAS: Orillas de Río San Juan, region de La Yeguada, 645 m, *Correa 1908* (MO).

5. CAVENDISHIA

Cavendishia Lindl., Bot. Reg. 21: sub *pl. 1791.* 1836. TYPE: *C. nobilis* Lindley.

?*Chupalon* Adans., Fam. Pl. 2: 164. 1763.
Socratesia Klotzsch, Linnaea 24: 22. 1851. TYPE: *S. melastomoides* Klotzsch.
Polyboea Klotzsch, Linnaea 24: 24. 1851.
Proclesia Klotzsch, Linnaea 24: 32. 1851.

Erect *shrubs*, evergreen, epiphytic or terrestrial; bark thin, cracking longitudinally. *Leaves* alternate, simple, estipulate, plinerved or pinnate, coriaceous, marginally entire and revolute, both surfaces usually with multicellular, reddish or blackish, slightly sunken, glandular trichomes to 0.2 mm long, if glabrescent appearing punctate. *Inflorescence* axillary, racemose or subfasciculate, usually solitary, encircled at the base by a progression of bracts, the smallest bracts minute and triangular, the largest conforming to the shape and size of the individual floral bracts, the inflorescence bracts few to numerous, imbricate, coriaceous, smooth or minutely striate or muricate, marginally scarious and usually minutely glandular fimbriate; floral bracts solitary at base of pedicel, usually large and showy; pedicels cylindric, bibracteolate near the base or rarely midway up the pedicel; bracteoles chartaceous or coriaceous. *Flowers* with the hypanthium articulate at the pedicel, constricted at the base of the limb, the tube basally expanded or not, fused with the ovary wall, the limb erect or spreading, free from the ovary wall, 5-lobed; corolla tubular, usually carnose when fresh, 5-lobed, the lobes valvate or conduplicate valvate, usually flaring at anthesis; stamens 10, subequal or rarely unequal, subequalling the corolla, the filaments ligulate, usually distinct, rarely slightly coherent at the extreme base at anthesis, alternately unequal, the anthers alternately unequal, the thecae smooth or slightly granular, the tubules about the same width as the thecae and about twice as long, dehiscent by introrse, elongate clefts; ovary inferior, 5-locular, surmounted by a flat of cupuliform, nectariferous disc, the style filiform, straight or sigmoid, usually glabrous, the stigma minutely 5-lobed, truncate but slightly flaring at anthesis. *Fruit* a juicy, spherical, dark blue black berry; *seeds* many, minute, 0.5–1 mm long, the testa ruminate.

Cavendishia may be easily recognized by usually large, brightly colored floral bracts and by stamens with alternately unequal filaments and anthers.

Cavendishia is a neotropical genus of epiphytic and terrestrial shrubs with approximately 150 species. They are distributed from the Mexican state of Oaxaca south through montane Central America to Bolivia, and as far east as Surinam. The greatest concentration of species occurs in Colombia where approximately 70 species have been recognized. In Central America the genus is most abundant in Panama and Costa Rica where all of the 30 species recognized occur. Most species have narrow distributional ranges; many are restricted to single mountain ranges or to one particular peak. *Cavendishia crassifolia* has

the greatest geographic distribution of the Central American species ranging from Mexico to Panama. *Cavendishia callista* is found in Guatemala and again in Costa Rica and Panama.

Literature:

Luteyn, J. L. 1975. The genus *Cavendishia* (Vacciniaceae) in Costa Rica. Brenesia 6: 9–18.

———. 1976. A revision of the genus *Cavendishia* (Vacciniaceae) in Mexico and Central America. Mem. New York Bot. Gard. 28(3): 1–138.

a. Leaves sessile to subsessile, amplexicaul with strongly cordate bases; calyx lobes imbricate ..... 7. *C. complectens*

aa. Leaves subsessile to long petiolate, never amplexicaul, and with variously shaped but never strongly cordate bases; calyx lobes not imbricate, or if basally contiguous then the leaves long petiolate.

b. Calyx tube usually conspicuously enlarged basally or with a wide spreading basal rim, if inconspicuously enlarged then with globular glands; calyx lobes and bracteoles marginally, apically, or completely glandular-callose thickened or with intermittent stout, oblong glandular thickenings (*C. quercina*), the lobes never glandular fimbriate, the bracteoles rarely glandular fimbriate and if with glandular fimbriae then the calyx and corolla pilose and the leaves less than 7 cm long (bracteoles eglandular in *C. santafeënsis*); calyx lobes erect after anthesis.

c. Leaves apically rounded, obtuse, if acute then the leaves usually less than 7 cm long; corolla 15 mm long or less; calyx sinuses usually ciliate; calyx lobes with several, small, intermittent, stout glandular thickenings which sometimes coalesce distally to form short oblong glandular thickenings ..... 19. *C. quercina*

cc. Leaves apically acuminate to caudate acuminate, if acute then leaves mostly more than 7 cm long; corolla usually 15 mm long or more; calyx sinuses glabrous; calyx lobes completely callose thickened, or with distinct thickenings running the length of the margin.

d. Plants with globular, peltate, red glands to 0.7 mm in diameter on calyx tubes, floral bract margins, bracteole margins, pedicels, and rachises; leaves with scattered globular glands 0.1–0.2 mm in diameter along the upper surface and the margin, these caducous leaving a reddish or blackish, papillate scar; calyx tube little or not enlarged.

e. Leaves linear lanceolate to linear elliptic, about 9 times as long as broad, usually without globular glands at maturity; bracteoles ca. 25 mm long, located just below the calyx; Bocas del Toro and Veraguas (Atlantic slope) Provinces ..... 17. *C. pseudostenophylla*

ee. Leaves elliptic, lance elliptic to ovate lanceolate, less than 4 times as long as broad, with globular glands at maturity; bracteoles less than 5 mm long, located at the base of the pedicel; Chiriquí Province.

f. Leaves less than 10 cm long and 4 cm wide, apically caudate acuminate; rachis less than 5 cm long, ca. 1 mm in diameter at its base, with 6–9(–11) flowers; floral bracts less than 30 mm long; bracteoles linear; pedicels less than 10 mm long; calyx 3.5–4.5 mm long, the tube surface not obscured by globular glands, the lobes entirely callose thickened; corolla less than 25 mm long; style less than 25 mm long ..... 6. *C. chiriquiensis*

ff. Leaves greater than 10 cm long, 4 cm or more wide, apically acuminate; rachis greater than 8 cm long, ca. 5 mm in diameter at its base, with 11–21 flowers; floral bracts 30 mm long or longer; bracteoles ovate to lanceolate; pedicels 10 mm or more long; calyx 4–6 mm long, the tube surface obscured

by globular glands, the lobes marginally callose thickened; corolla 25 mm or more long; style 25 mm long or more ..... 16. *C. panamensis*

dd. Plants without globular, peltate, red glands; leaves without globular glands; calyx tube conspicuously basally enlarged.

g. Calyx lobes with oblong, callose-thickened glands the entire length of each margin; bracteoles 3 cm or more long; Veraguas Province ..... 21. *C. santafeënsis*

gg. Calyx lobes completely glandular callose thickened over the entire surface, not just marginally; bracteoles less than 1 cm long.

h. Leaves linear to elliptic lanceolate, 5–6 times as long as broad, pinnately veined, marginally strongly revolute; floral bracts marginally callose thickened for the distal ⅔; bracteoles continuous with the pedicels ..... 22. *C. stenophylla*

hh. Leaves variously shaped but never linear, less than 5 times as long as broad, plinerved, marginally nearly flat; floral bracts marginally eglandular; bracteoles articulated with the pedicels.

i. Floral bracts apically acute or rounded, never emarginate; rachis elongate, 3–12(–20) cm long, rarely shorter (and then floral bracts 6–10 mm long).

j. Corolla pubescent; floral bracts (15–)25–40(–50) mm long.

k. Corolla densely sericeous, white; rachis (4–) 6–12(20) cm long with 20–35 flowers; petioles densely pilose to glabrate; Veraguas, Coclé, and Panamá Provinces ..... 4. *C. callista*

kk. Corolla short pilose, purple; rachis 3–6(–9) cm long with (7–)11–16(–20) flowers; petioles glabrous even when young; Chiriquí Province ..... 2. *C. atroviolacea*

jj. Corolla glabrous; floral bracts 6–20 mm long.

l. Corolla 18–20 mm long, lobes callose thickened; bracteoles lanceolate; floral bracts 15–20 mm long; Darién Province ..... 15. *C. morii*

ll. Corolla 28–32 mm long, lobes not callose thickened; bracteoles broadly ovate to hemispheric; floral bracts 6–10 mm long; Chiriquí Province ..... 14. *C. melastomoides* var. *coloradensis*

ii. Floral bracts apically rounded and usually noticeably emarginate; rachis short (0.3–)0.6–2(–3.5) cm long.

m. Corolla 27–43 mm long; stamens 24.5 mm long or more; style more than 30 mm long; floral bracts (2–)3–6(–7) cm long, dark red in bud but turning pink or pale purplish red at anthesis; calyx 7–13 mm long, the limb including the lobes (4–)5–7.5 (–9) mm long and cylindric to slightly spreading ..... 13. *C. megabracteata*

mm. Corolla 20–24(–30) mm long; stamens 24.5 mm long or less; style less than 30 mm long; floral bracts 1.5–3(–4) cm long, green; calyx 5–7(–10) mm long, the limb including the lobes 2.5–4.5(–6) mm long and campanulate to cylindric ..... 23. *C. subfasciculata*

bb. Calyx tube basally rounded, truncate, or with a narrow rim, never conspicuously enlarged, the rim never flaring, never with globular glands on the surface of the tube; calyx lobes and bracteoles usually with marginal, caducous glandular fimbriae to 0.2 mm long, never callose thickened (calyx lobes eglandular in *C. darienensis*; bracteoles eglandular in *C. fusiformis*); calyx lobes connivent or erect after anthesis.

n. Calyx limb and floral bracts conspicuously striate; bracteoles striate and

5–20 mm long, if smooth then more than 20 mm long; floral bracts persistent in fruit.

o. Bracteoles smooth, more than 20 mm long, apically rounded and emarginate; corolla more than 30 mm long; stamens about ⅓ as long as the corolla; calyx limb more than 8 mm long; Darién Province ---------- 10. *C. fusiformis*

oo. Bracteoles striate, less than 20 mm long, apically rounded, acute or acuminate but never emarginate; corolla less than 20 mm long; stamens about as long as the corolla; calyx limb less than 8 mm long.

p. Leaves pinnately veined; floral bracts 13 mm long or less, obovate to semiorbicular; bracteoles 9 mm long or less; corolla 10 mm long or less ---------- 3. *C. axillaris*

pp. Leaves plinerved; floral bracts 13 mm long or longer, lanceolate to elliptic or ovate elliptic, rarely obovate or semiorbicular; bracteoles usually more than 10 mm long; corolla more than 10 mm long.

q. Twigs, leaves, rachises, pedicels, floral bracts, bracteoles, calyces, and corollas short pubescent; rachis more than 8 cm long; floral bracts lanceolate, apically long acuminate; calyx lobes marginally eglandular; corollas nonstriate; Darién Province ---------- 9. *C. darienensis*

qq. Plants glabrous throughout; rachis less than 5 cm long; floral bracts elliptic, ovate elliptic, obovate, or rarely semiorbicular, apically acute; calyx lobes marginally glandular fimbriate; corollas conspicuously striate; Coclé and Panamá provinces ---------- 1. *C. allenii*

nn. Calyx limb and floral bracts never striate; bracteoles smooth, never striate, rarely more than 5 mm long; floral bracts caducous soon after anthesis.

r. Leaves apically obtuse or rounded, usually less than 6 cm long; calyx lobes erect after anthesis; rachis subfasciculate, less than 1 cm long with 3–6(–7) flowers; pedicels 1.5–2(–5) mm long ---------- 5. *C. capitulata*

rr. Leaves apically acuminate or sharply acute, usually greater than 6 cm long; calyx lobes connivent or erect after anthesis; rachis elongate, usually more than 1 cm long with 6 or more flowers; pedicels more than 3 mm long.

s. Calyx 9–14 mm long.

t. Leaves glabrous, very thick coriaceous, the margins so tightly revolute as to be obscured from view; calyx glabrous; style 10–11 mm long; plants reportedly with odor of wintergreen; Cerro Jefe, Panamá Province ---------- 20. *C. revoluta*

tt. Leaves pilose on both surfaces, membranaceous to coriaceous but not conspicuously thickened, the margins only slightly revolute; calyx densely pilose; style ca. 21 mm long; plants lacking the odor of wintergreen; Cerro Tacarcuna, Darién Province ---------- 11. *C. gentryi*

ss. Calyx less than 9 mm long.

u. Corolla 8–10(–12) mm long; floral bracts 7–13 mm long; rachis 4–15(–20) cm long; Darién Province ---------- 12. *C. laurifolia*

uu. Corolla (12–)15–25 mm long; floral bracts (11–)17–40 mm long; rachis 1–5(–8) cm long.

v. Calyx pubescence of densely matted trichomes; plants including mature berry persistently short, white pilose; corollas white or white with a pinkish hue; floral bracts pale green often with a pinkish hue; Chiriquí Province ---------- 18. *C. pubescens*

vv. Calyx glabrous or trichomes usually sparse and short, never densely matted; plants glabrous or variously pubescent but mature berry always glabrous; corollas pink to red with white tips; floral bracts red; Chiriquí, Veraguas, Coclé, and Panamá provinces ---------- 8. *C. crassifolia*

1. **Cavendishia allenii** A. C. Smith, Ann. Missouri Bot. Gard. 28: 445. 1941. TYPE: Panama; Coclé, N of El Valle de Antón, 1,000 m, *Allen 2471* (A, holotype; photo of type, DUKE, NY).

Epiphytic *shrub* to 1 m tall, glabrous throughout; stem base to 1.5 cm in diameter; branches terete or subterete, smooth or somewhat striate when immature, reddish brown, bark reddish or grayish brown. *Leaves* elliptic or ovate elliptic, (3.5–)5–11.5 cm long, 2–7 cm wide, basally rounded or somewhat subcordate, apically acute or broadly obtuse, dull olive brown and shining when dry; inconspicuously 3–5(–7)-plinerved, the midrib impressed above, raised beneath, prominent on both the surfaces, the primary lateral nerves thin, raised on both the surfaces, far removed from the midrib, the secondary nerves thick, raised and conspicuous above causing the leaf to appear pinnately veined; petioles terete, rugose, 1–4 mm long, 1–3 mm in diameter. *Inflorescences* tightly congested racemes, 8–16 flowered basally encircled by striate bracts, the rachis bluntly angled, smooth or striate, often muricate, 1.5–4 cm long, ca. 2 mm in diameter at anthesis, elongating to 6 cm in the fruit; floral bracts conspicuously striate, concave, elliptic, ovate elliptic or obovate, rarely semiorbicular, basally rounded to truncate, slightly auriculate, apically acute, sometimes broadly so, the margins often so tightly revolute that the bracts appear sharply acuminate, (13–)15–20 mm long (6–)8–12(–18) mm wide, rose or salmon pink or pale green with a pinkish hue, marginally glandular fimbriate, the fimbriae early caducous, the bracts persisting as the berry matures; pedicels subterete, 1–1.5(–3) mm long, 1–1.5 mm in diameter; bracteoles striate, concave basally, ovate lanceolate or oblong, apically rounded or acute, 11–13(–17) mm long, (3–)5–7 mm broad, marginally glandular fimbriate, tightly imbricate in bud, completely enclosing the calyx, often persistent in fruit. *Flowers* with the calyx 8–12(–15) mm long, pink, the tube barrel-shaped or globose at anthesis, smooth or slightly rugose, not enlarged, 2–4.5(–5) mm long, 2–4 mm in diameter, the limb cylindric, striate, (3.5–)5–7(–9) mm long including the lobes, the lobes triangular or nearly oblong, acute, or apiculate, 1.5–2 mm long and broad, erect after anthesis, marginally glandular fimbriate and slightly scarious, the sinus acute to obtuse, corolla tubular, slightly wider medially, conspicuously striate, 11.5–16 mm long, 3.5–4 mm in diameter, pale green with a yellow tip, the lobes oblong, bluntly acute, 2–3.5 mm long, slightly thickened at the tip, erect at anthesis; stamens 9.5–13 mm long, the filaments coherent at base, distally pubescent, alternately 2.5–4 mm, 3.5–5 mm long, the anthers including the tubules alternately 7–10.5 mm and 8.5–12 mm long, the thecae 2–3.5 mm long; style 11.5–14.5 mm long. *Berry* 15 mm in diameter.

Cavendishia allenii is the only *Cavendishia* in Central America with a corolla that is conspicuously nerved or striate and pale green with a yellow tip. It is endemic to central Panama, being found between 200–1,000 m elevation. Its relationship to *C. darienensis* is discussed under that species.

COCLÉ: El Valle de Antón, 600 m, *Allen 2068* (MO); *Allen 2278* (GH, MO, US). El Valle, 800 m, *Allen 2308* (MO). Trail to Las Minas, N of El Valle de Antón, 1000 m, *Allen 2471* (A). N of El Valle de Antón, La Mesa, 1000 m, *Allen 2834* (A); *Allen 2897* (A, MO).

Ridge of Loma del Tigre, 865 m, *Allen 4481* (MO). Cloud forest on slopes of Cerro Pilón near El Valle, 700–900 m, *Duke 12162(2)* (MO). Cerro Pilón, 890 m, *Dwyer 8328* (MO). Mountains beyond La Pintada, 400–600 m, *Hunter & Allen 572* (F, G, MO, S). Trail beyond La Mesa towards Los Llanos, 800–860 m, *Luteyn 3173* (DUKE, NY); *Luteyn 4100* (DUKE, MICH, NY). COLÓN: E of Santa Rita ridge, *Correa 646* (MO). Santa Rita Ridge road, 4 mi from Transisthmian Highway, 500 m, *Gentry et al. 8861* (NY). PANAMÁ: 19 km along Cartí road, 500 m, *Busey 885* (DUKE). Cerro Jefe, 0.5 km S of summit, *Busey & Croat 266* (MO). La Eneida, *Dressler 3229* (MO). Cerro Jefe, *Duke 9427* (MO); *Dwyer et al. 7299* (MO). Cerro Jefe to La Eneida, 650–890 m, *Dwyer et al. 8224* (MO). Cerro Jefe, Altos de Pacora, 800–900 m, *Gentry & Mori 13431* (NY). 10–16 km from Panamerican Highway on El Llano-Cartí-Tupile road, *Kennedy 2507*; *Kennedy et al. 2415*; *Liesner 1149, 1322* (all MO); *Luteyn & Wilbur 4664* (DUKE, MO); *Luteyn & Wilbur 4682* (DUKE). 5–10 km NE Altos de Pacora, 750 m, *Mori & Kallunki 4954* (NY). 10–12 km N of Inter-American Hwy along El Llano-Cartí-Tupile road, ca. 500 m, *Wilbur & Luteyn 19504* (DUKE). Beyond Cerro Azul, ca. 5.5 mi on road to La Eneida, 830–925 m, *Wilbur & Teeri 13630* (DUKE). Trail off Cerro Jefe road, 0.4 km beyond turnoff to Altos de Pacora, *Witherspoon & Witherspoon 8586* (MO, NY).

2. **Cavendishia atroviolacea** Luteyn, Brittonia 28: 49. 1976. TYPE: Panama; *Luteyn 3045* (DUKE, holotype; F, GH, LL, MICH, MO, NY, PMA, UC, US, isotypes).

Epiphytic *shrub* 1–3 m tall, stem base to 2.5 cm in diameter; mature branches terete to subterete, smooth or minutely striate, glabrous, 6–7 mm in diameter, often red dorsally and green ventrally when fresh; bark brown, but drying yellowish, grayish, or reddish brown, the immature branches and twigs of the new growth subterete to bluntly angled, minutely striate, glabrous, reddish brown when dry. *Leaves* lanceolate to lance elliptic, rarely oblanceolate or ovate, (3–)8–12(–18) cm long and 1–4(–6) cm broad, basally rounded, obtuse, cuneate or rarely subtruncate, apically acuminate, olive tan or silvery green when dry, glabrous or rarely with a few hairs at the base of the midrib on the upper surface; (3–)5(–7)-plinerved, veins impressed above or rarely veinlets and the outer pair of lateral veins raised, the midrib raised and prominent beneath, the lateral veins raised, prominent to obscure beneath, the veinlets slightly raised, usually obscure beneath; petioles terete or often flattened adaxially, rugose, (4–)6–15 mm long, (0.7–)1–1.5(–2.5) mm in diameter, glabrous, green suffused with maroon, drying reddish brown. *Inflorescence* (7–)11–16(–20) flowered, cylindric to fusiform in bud, rachis long tapering, cylindric, bluntly angled, minutely striate, viscid, glabrous, 3–6(–9) cm long, 2–5 mm in diameter, pink to pinkish white when fresh; floral bracts rarely translucent when dry, glabrous, smooth or reddish papillate abaxially, oblong to oblanceolate, rarely obovate or somewhat spatulate, basally narrowed and truncate, apically rounded to acute, (2–)2.5–4(–5) cm long, 1–2 cm broad, deep violet or maroonish purple, often appearing black; pedicels swollen distally, striate or ribbed, glabrous, (6–)9–13(–16) mm long, 0.7–(–1.5) mm in diameter, pink to pinkish white when fresh; bracteoles lanceolate to linear lanceolate, rarely ovate, 2–4(–5.5) mm long, 0.6–1(–2) mm broad, basally slightly auriculate, apically acuminate and glandularly callose thickened in the distal third, purplish pink when fresh. *Flowers* with the calyx glabrous, (6–)7–11(–13.5) mm long, the tube cylindric, coarsely ribbed, (2–)2.5–4(–5.5) mm long, basally (2.5–)3–6(–6.5) mm in diameter, basally enlarged and deeply lobed, the lobes straight or flaring outward and extending well be-

low the basal articulation, pinkish red to purplish at anthesis turning pale green post anthesis, the limb cylindric or somewhat spreading, weakly ribbed or minutely papillate, (3.5–)5–8 mm long including the lobes, pinkish red, the lobes triangular, 1–2(–2.5) mm long, and 2–2.5 mm broad, erect after anthesis, glandular callose thickened without, dark reddish purple or green; sinus obtuse to broadly rounded; corolla slightly constricted basally, narrowed to the throat, sometimes translucent when dry, (25–)30–38(–45) mm long, 5–8 mm in diameter, pilose with short, white trichomes, the tube whitish purple at the constricted base, purple to dark purple above, the limb and the lobes pale purple, the lobes oblong, obtuse, 1.5–2 mm long, strongly reflexed at anthesis; stamens 24–39 mm long, the filaments glabrate or moderately pilose distally, alternately 3.5–6 mm and 7.5–14.5 mm long, white, the anthers including tubules alternately 16.5–27.5 mm and 22.5–35.5 mm long, orange, the thecae 6–13.5 mm long; style 35–46 mm long. *Berry* not seen.

Cavendishia atroviolacea can be recognized by the large, violet to very dark maroonish purple floral bracts which are striking in the living condition. This character along with a purple corolla, greenish to reddish green calyx, and many flowered inflorescences combine to make it one of the most beautiful species in the Chiriquí highlands. This species is a near Panamanian endemic having been collected elsewhere only once on the southwest slopes of Cerro Pando along the border between Panama and Costa Rica. *Cavendishia atroviolacea* seems most closely related to the widespread *C. callista*.

CHIRIQUÍ: NW side of Cerro Punta, Las Nubes, 2000–2400 m, *Almeda 1535* (DUKE, NY); *Croat 10459, 22414* (both MO), *26465* (MO, NY). Slopes of Cerro Punta, 2000 m, *Gentry 5878* (MO). NW side of Cerro Punta, Las Nubes, 2000–2400 m, *Luteyn 3045* (DUKE, F, GH, LL, MICH, MO, NY, PMA, UC, US), *3804* (DUKE, F, MICH, MO, NY, US). Bajo Chorro Trail, 2360–2500 m, *Luteyn 3059, 3814* (both DUKE). Monte Lirio, 1300–1900 m, *Seibert 176* (US). NW side of Cerro Punta, Las Nubes, 2000–2400 m, *Utley et al. 244* (DUKE, NY). Valley of the upper Río Chiriquí Viejo, 1300–2000 m, *White & White 23* (MO). NW side of Cerro Punta, Las Nubes, 2000–2400 m, *Wilbur & Almeda 17072* (DUKE, F, GH, MO, NY, US); *Wilbur & Teeri 13202* (DUKE). Along Río Chiriquí Viejo, ridge of Cerro Respinga, 2160 m, *Wilbur & Teeri 13117* (DUKE). NW side of Cerro Punta, Las Nubes, 2000–2400 m, *Wilbur et al. 11954* (DUKE). Valley of the upper Río Chiriquí Viejo, 1300–2000 m, *Wilbur et al. 13036* (DUKE, F, MO, NY).

3. **Cavendishia axillaris** A. C. Smith, Contr. U. S. Natl. Herb. 28: 493. 1932. TYPE: Colombia; Bolívar, 2,300–2,700 m, *Pennell 4375* (NY, holotype; photo of type, DUKE).

C. gaultherioides A. C. Smith, Ann. Missouri Bot. Gard. 28: 444. 1941. TYPE: Panama; Coclé, La Mesa, N of El Valle de Antón, 1000 m, *Allen 2375* (A, holotype; photo of holotype, DUKE, NY; MO, isotype).

Terrestrial or epiphytic *shrubs*, 0.5–1.5(–3) m tall, glabrous throughout when mature; stem base 1–2.5 cm in diameter; mature branches often arching, terete to bluntly angled, smooth or striate; bark often reddish above and brown to grayish brown beneath; immature branches and twigs of new growth terete or flattened, densely puberulent, glabrescent. *Leaves* ovate, obovate, elliptic or suborbicular, 4.5–10.5(–17) cm long, (2.5–)4–11 cm broad, basally cuneate, obtuse, rounded or subcordate and then often slightly amplexicaul, apically obtuse

or rounded, grayish to brownish green above and tan to olive green beneath when dry, pinnately veined, the midrib elevated on both the surfaces, the proximal ⅓ conspicuously thickened, 3–5 times thicker than the narrowed and impressed distal portion, the lateral nerves arcuate, anastomosing near the margin, impressed above, sometimes strongly so, raised and prominent beneath, the leaves hence frequently bullate, the veinlets impressed or slightly raised above, elevated beneath, newly unfolding leaves puberulent but later glabrate; petioles subterete, striate or rugose, 1.5–3(–5) mm long, 2.5–3.5(–4.5) mm in diameter, dark reddish brown. *Inflorescences* solitary racemes or rarely 2–5 per axil, tightly racemose, the floral internodes ca. 1 mm long, (5–)9–15(–47) flowered, capitate or cylindric at anthesis, encircled at the base by striate bracts, the rachis terete or bluntly angled, 1–2(–8) cm long, the floral nodes swollen; floral bracts smooth or muricate, striate when dry with conspicuously thickened, dichotomously branching veins, obovate to semiorbicular, basally truncate, apically rounded or acute, the apex usually splitting deeply, 7–10(13) mm long, (5.5–)8–11(–13) mm broad, marginally scarious and densely glandular fimbriate, concave, tightly appressed to and concealing the calyx and the lower portion of the corolla at anthesis, often persistent until after the berry has matured; pink to dark rose red; pedicels to 1 mm long, 1 mm in diameter, rarely with few cartilaginous teeth distally; bracteoles smooth or muricate but conspicuously striate when dry, elliptic oblong, basally truncate, apically rounded, (5–)7–9 mm long, (2–)4–6 mm wide, marginally scarious and densely glandular fimbriate, concave and strongly keeled, rarely flat, imbricate and completely enveloping the perianth in bud, tightly appressed to the calyx at anthesis, pink to dark rose red. *Flowers* with the calyx (4.5–)6–7.5 mm long, the tube cylindric, smooth to rugose, nonexpanded basally (1.5–)2.5–3 mm long, 2.5 mm in diameter, pink to pale green, the limb spreading to campanulate, conspicuously striate within and without when dry, (2.5–)3.5–4(–5) mm long including the lobes, pale green, the lobes ovate to triangular, rarely oblong, acute, 1–2 mm long and 1.5–3 mm wide, erect after anthesis, the margins glandular fimbriate and occasionally slightly imbricate at the base, pale green and occasionally marginally pink, the sinuses acute or narrowly obtuse; corolla cylindric or slightly bottleshaped, narrowed at the throat, (6.5–)9–10 mm long, 3.5–4(–6) mm in diameter, often glandular fimbriate distally, white to pale green in the basal ⅓, green to yellowish green in median ⅔, the limb and the lobes pale green, the lobes oblong to narrowly triangular, obtuse, 1–2 mm long; stamens 6–8.5 mm long, the filaments short puberulent distally, alternately 1.5–2.5 mm and 2.5–3.5 mm long, the anthers including tubules alternately 4–6 mm and 5–6.5 mm long, the thecae 1.5–2.5 mm long; style 8–9 mm long. *Berry* 9–10 mm in diameter.

Cavendishia axillaris ranges from Costa Rica and Panama south into Colombia and adjacent Ecuador. In Central America it is generally found between 700–1,500 meters. It is well characterized by its pinnately veined, subsessile leaves, compact inflorescences, its conspicuously nerved floral bracts and bracteoles which are tightly appressed to the calyx, and by its small flowers. Numerous Central American collections have been misidentified as *C. complectens*. Together they share pinnately veined leaves and compact inflorescence, although

the rachis of *C. complectens* may lengthen considerably after anthesis. They are most easily separated by the fact that the leaves of *C. complectens* are strongly amplexicaul and the calyx lobes are reniform and broadly imbricate, whereas in *C. axillaris* the leaves are never amplexicaul, the calyx lobes are triangular to ovate and are only rarely imbricate at the very base.

CHIRIQUÍ: Between Pinola and Quebrada Hondo, Chiriquí Trail, *Kirkbride & Duke 879* (MO). COCLÉ: Hills N of El Valle de Antón, 1000 m, *Allen 2170* (A); *Allen 2329* (A, MO). La Mesa, N of El Valle de Antón, *Allen 2375* (A, MO); *Allen 2736, 2787* (both A). Hills N of El Valle de Antón, 1000 m, *Allen 3559* (G, MO). 39 km from Interamerican Highway along El Valle dirt road, *Correa 327* (MO). La Mesa, N of El Valle de Antón, *Croat 14393* (MO, NY). Along road past Furlong's finca, due N of Cerro Pilón, 880 m, *Croat 37549* (NY). Cloud forest on Cerro Pilón, 700–900 m, *Duke 12175* (MO). 9 km from El Valle market beyond Sr. Furlong's finca, *Kennedy et al. 3188* (MO). N of El Valle, beyond La Mesa towards Los Llano, 800–850, *Luteyn 3157, 4112* (both DUKE); *Luteyn & Kennedy 1689* (DUKE). Roadside, La Mesa, 4 km N of El Valle, 875 m, *Nee & Dwyer 9169* (NY). Cerro Pilón above El Valle, 620 m, *Porter et al. 4467, 4639* (both MO). La Mesa, N of El Valle de Antón, *Wilbur et al. 11116* (DUKE). DARIÉN: Cerro Tacarcuna massif between summit camp on westernmost ridge and Pico Tacarcuna, 1650–1800 m, *Gentry, Leon & L. Forero 16916* (NY). Elfin forest at top of W peak of Cerro Tacarcuna massif, 1800–1850 m, *Gentry & Mori 13979* (MO, NY). VERAGUAS: Santa Fé, slopes of Cerro Tute, 925 m, *Allen 4343* (G, MO, US). Road between Escuela Agrícola Alto Piedra and Río Dos Bocas, 730–770 m, *Croat 25913* (MO). 20 km NW Santa Fé, 650–800 m, *Kennedy & Dressler 3420* (NY). Road past Escuela Agrícola Alto Piedra on Pacific side, 800–1000 m, *Liesner 862* (MO); *Luteyn & Wilbur 4578* (DUKE, F, MO, NY). NW of Santa Fé, 1–4.2 km from Escuela Agrícola Alto Piedra, *Mori & Kallunki 4026* (WIS), *4827* (NY). 6–7 km W of Santa Fé, road past agricultural school, *Nee 9714* (NY). Along first branch of Río Santa Maria by road from Santa Fé, *Witherspoon & Dressler 8922* (MO, NY).

4. **Cavendishia callista** Donnell Smith, Bot. Gaz. (Crawfordsville) 20: 5. 1895. TYPE: Guatemala; Alta Verapaz, between Cobán and Samac, 1,400 m, *Tuerckheim 941* (US, lectotype; photo of lectotype DUKE, NY; F, G, GH, NY, isolectotypes).

C. longiflora Donnell Smith, Bot. Gaz. (Crawfordsville) 37: 420. 1904. TYPE: Costa Rica; San José, Alto de La Palma, *Tonduz 7391* (US, lectotype; photo of lectotype, DUKE; BM, F, G, GH, NY, US, isolectotypes).

C. bullata A. C. Smith & Standley, Contr. U.S. Natl. Herb. 28: 453. 1932. TYPE: Costa Rica; Cartago, Naranjo, *Stork 1789* (F, holotype; photo of holotype, DUKE, NY; G-fragments from holotype; MICH, isotype).

Epiphytic and terrestrial *shrubs*, 1.5–3 m tall; stem base ca. 2.5–5 cm in diameter; mature branches and twigs of new growth bluntly angled to terete, often glaucous, glabrous to densely pilose, often glabrescent, the trichomes tan to yellowish and 0.5–2 mm long, bark brown to reddish brown. *Leaves* ovate, lanceolate, elliptic, oblong, rarely obovate, (5–)7–26(–32) cm long, (1–)2–10(–13) cm wide, basally obtuse, rounded or truncate, often slightly cordate apically acute to long acuminate sometimes abruptly short acuminate, tan, olive brown, or reddish brown when dry, glabrous to moderately short pubescent on the lamina above, glabrate to densely pubescent beneath especially along the nerves; (3–)5(–9)-plinerved with the midrib and the lateral nerves shallowly to deeply impressed above, raised and conspicuous beneath, the veinlets usually slightly elevated on both the surfaces but secondary lateral nerves and veinlets often deeply impressed above giving the lamina a strikingly bullate appearance; petioles subterete, rugose, (4–)6–16(–22) mm long, (1–)2–3(–5) mm in diameter,

glabrous to densely pilose with trichomes to 1.5 mm long. *Inflorescence* viscid, 20–35(–52) flowered, encircled at the base by bracts, rachis bluntly angled, longitudinally ribbed, glabrous or infrequently densely sericeous, 4–12(–20) cm long, 4–6(–10) mm in diameter, rose colored but drying yellowish to orangish brown, rarely with minute, reddish, clavate glands especially at the base of the floral bracts; floral bracts pink, smooth or muricate, glabrous, oblong, obovate or oblanceolate, basally narrowed and truncate, apically rounded to acute, the tips rarely reflexed, (1.5–)2–5(–6) cm long, 1–2.5(–3.5) cm broad; pedicels smooth or rugose, usually longitudinally ribbed, usually swollen at both ends, glabrous or infrequently densely sericeous, 6–15(–20) mm long, 0.5–1.5(–2) mm in diameter, rarely with sessile, reddish glands or cartilaginous teeth at the apex; bracteoles glabrous, infrequently conspicuously nerved, ovate lanceolate, basally somewhat auriculate clasping, 1–5(–7) mm long, 1–2(–3.5) mm wide, apically glandular callose thickened, rarely callose thickened for nearly the entire length. *Flowers* with the calyx glabrous or infrequently densely pilose, 5–9(–11) mm long, viscid, the tube cylindric, coarsely ribbed, rugose, often muricate, (1.5–)2–4(–5.5) mm long, strongly expanded basally, pinkish green, at anthesis becoming green, the limb cylindric or spreading, often striate, 3.5–6(–8) mm long including the lobes, dark rose at anthesis becoming pale rose to pink, the lobes triangular, 1–2.5(–4) mm long, 2–3 mm broad, erect after anthesis, usually completely glandular callose thickened, green to brownish green when fresh, the sinus obtuse to broadly acute; corolla narrowed to the throat, viscid, 1.5–3.5(–4) cm long, 4–8 mm in diameter, densely sericeous or rarely glabrous externally, moderately pilose or rarely glabrous within with translucent trichomes 0.5–1 mm long, the tube white or with a pinkish hue basally, the lobes triangular, 1–3 mm long, 2–3 mm wide, reflexed at anthesis, white with purple margins; stamens (13–)20–34 mm long, the filaments alternately (1.5–)3.5–4.5(–6) mm and (4.5–)8–12 mm long, short pilose distally, white to pink, the anthers including the tubules alternately (8.5–)15–26 mm and (11–)27–32 mm long, the tubules purplish orange, the thecae 5–20 mm long, orange; style (17–)20–35(–40) mm long, green. *Mature berry* not seen.

Cavendishia callista is distinguished by rose pink floral bracts, and densely sericeous, white corollas which have purple margined lobes. The species is quite variable with respect to leaf size and shape, texture, degree of bullateness and pubescence, as well as pubescence of the twigs and other vegetative organs. This species is known from Guatemala, Costa Rica and Panama.

COCLÉ: Hills N of El Valle de Antón, 1000 m, *Allen 2207* (MO), *3598* (F, G, MO, US). La Mesa above El Valle, 800 m, *Croat 25397* (MO). Along road past Furlong's Finca, N of Cerro Pilón, 880 m, *Croat 37570* (MO, NY). El Valle, *Dwyer 1944* (MO). Cerro Gaital Caracoral, 1000 m, *Dwyer & Correa 8937* (NY). Cerro Pilón, *Dwyer & Lallathin 8656* (MO). La Mesa, above El Valle, 800 m, *Luteyn 3158* (DUKE, MO). Trail to Las Minas, N of El Valle, *Luteyn 3160* (DUKE, F, GH, MO, NY). Road to La Mesa, 740–800 m, *Vaughan et al. 612* (MO). N rim of El Valle de Antón, near Cerro Turega, 650–700 m, *Woodson & Schery 193* (CAS, G, MO, NY, US). COLÓN: Santa Rita, *Dwyer et al. 9013* (MO). DARIÉN: Elfin forest near top of westernmost peak of Cerro Tacarcuna massif, 1720 m, *Gentry, Leon & L. Forero 16894* (NY). PANAMÁ: Beyond Cerro Jefe, Campo Tres, 700 m, *Croat 27052* (MO). Cerro Jefe, 890 m, *Dwyer & Gauger 7342* (DUKE, MO); *Luteyn 3207, 3971* (both DUKE). Altos de Pacora beyond Cerro Azul, *Mori et al. 6921* (MO, NY). Cerro Jefe, 890–1000 m, *Mori 6520*

(NY); *Tyson et al. 4353* (DUKE, MO). VERAGUAS: beyond Tres Brazos River, 11 km beyond Santa Fé, 650 m, *Croat 25626* (MO).

5. **Cavendishia capitulata** Donnell Smith, Bot. Gaz. (Crawfordsville) 25: 147. 1898. TYPE: Costa Rica; San José, La Palma, *Wercklé 11.565* (US, holotype; CR, isotype; photo of holotype DUKE, NY).

Erect, much branched, spreading, usually epiphytic *shrub* 0.5–1.5(–2) m tall, stem base 1–3(–15) cm in diameter; mature branches terete to bluntly angled, glabrous, bark brown, rusty brown or gray to almost black; immature branches and twigs of new growth bluntly angled, glabrous or densely hirsute with spreading, white or yellowish trichomes ca. 0.5 mm long, frequently with clavate, reddish glandular fimbriae ca. 0.1 mm long. *Leaves* obovate, oblanceolate, elliptic, oblong elliptic or ovate, 1.5–3(–6) cm long, 0.5–1.5(–3) cm wide, basally cuneate or rounded, apically rounded, obtuse or rarely abruptly tapering to a blunt tip, dull green or olive to grayish brown when dry, the young leaves densely puberulent, glabrate at maturity; 3–5(–7)-plinerved, the midrib impressed or slightly raised, conspicuous above, raised and conspicuous beneath, lateral nerves slightly raised and conspicuous or plane and obscure on both surfaces, the veinlets slightly raised, conspicuous or obscure above, usually obscure beneath; petioles smooth, striate or more commonly rugose, subterete or flattened, 1–3(–5) mm long and 0.5–1 mm in diameter, puberulent, glabrescent, brown, reddish brown or blackish. *Inflorescence* fasciculate, 3–6(–7) flowered; rachis glabrous, 1–3(–7) mm long, 1–1.5 mm in diameter; floral bracts smooth or muricate, glabrous, obovate, basally narrowed, apically rounded, shallowly emarginate or rarely acute 11–14(–19) mm long, 6.5–11 mm wide, purple to reddish purple, marginally scarious and sparsely fimbriate, rarely densely ciliate, frequently with scattered, short, thick, reddish brown, glandular fimbriae along the lamina; pedicels cylindric or obconic, rugose or obscurely ribbed, sometimes bluntly angled, glabrous or sparsely pilose distally, (0.5–)1.5–2(–5) mm long 1–1.5(–2.5) mm in diameter, rarely with reddish brown, glandular, distal fimbriae; bracteoles oblong to oblong elliptic, (1–)3–6(–8.5) mm long, 1–2 mm wide, basally truncate, apically obtuse, purple, marginally scarious and densely glandular fimbriate with fimbriae to 0.8 mm long. *Flowers* with the calyx 4.5–7.5 mm long, the tube cylindric or barrel-shaped, often pentagonal in cross section, smooth or minutely rugose, 1–3 mm long, 2–3 mm in diameter, slightly enlarged with a narrow rim or collar basally, green to purple, sometimes with scattered, reddish brown, glandular fimbriae, the limb erect, somewhat spreading or campanulate, 1.5–4 mm long including the lobes, green to greenish white, the lobes triangular, obtuse to acute, 0.5–1.5 mm long, 1.5–2 mm wide, erect or somewhat connivent after anthesis, densely glandular fimbriate with fimbriae to 0.2 mm long, the sinuses broadly rounded or obtuse, rarely acute; corolla constricted basally, narrowed to the throat, 10–16 mm long, 4–5 mm in diameter, glabrous, the basal ¼ white or pale red, the middle ½ purple or reddish purple, the distal ¼ white, the lobes white, triangular, obtuse, 1 mm long; stamens 9–14.5 mm long, the filaments glabrous or distally with scattered hairs,

alternately either 1.5–3 mm or 3–6 mm long, the anthers including tubules alternately 5.5–10 mm and 7.5–12.5 mm long, the thecae 2–3 mm long; style (9.5–)11–15.5 mm long, the stigma somewhat peltate. *Berry* 5–7 mm in diameter.

Cavendishia capitulata ranges from Costa Rica to Panama and is found between 350–2,700 m elevation. It is distinctive despite the fact that the leaves are quite variable with respect to length and width. In Costa Rica and western Panama the leaves are usually narrowly oblong or elliptic, 2–2.5 cm long, 0.5–1 cm broad, and both the apex and the base are rounded, but the leaves may be obovate oblanceolate with cuneate bases. In central and eastern Panama, from Santa Fé de Veraguas to the Province of Darién, the leaves are usually much longer and broader, averaging 2.5–5.5 cm long and 1–2.5 cm broad. However, in floral characters these geographical variants are similar in all respects, and infraspecific recognition of these variants is not warranted.

BOCAS DEL TORO: Between Criollo and Quebrada Higueron on Chiriquí Trail, *Kirkbride & Duke 778* (MO, NY). BOCAS DEL TORO-CHIRIQUÍ border: Cerro Colorado copper mining road, N of San Félix, *Mori & Kallunki 5790, 5989* (both NY). CHIRIQUÍ: Trail from Cerro Punta to headwaters of Río Caldera, 2250–2500 m, *Allen 1434* (MO). Cloud forest at Monte Rey above Boquete, *Croat 15774* (MO); *Croat & Porter 15679* (MO). Cloud forest along continental divide on Cerro Colorado along upper mining road 20–28 mi from San Félix, 1200–1500 m, *Croat 33317* (MO, NY). Bajo Chorro, 1840 m, *Davidson 92* (A, F, US), *120* (A, F, US). Las Nubes, 1900–2200 m, *Luteyn 3044* (CAS, DUKE, LL, MICH, MO, NY, PMA). Bajo Chorro, 2190–2210 m, *Luteyn 3048* (DUKE, NY). Bajo Mono, NW of San Ramón, 1600–1700 m, *Luteyn 3727* (DUKE, MO, NY). E slopes of Cerro Horqueta, 1700–1800 m, *Luteyn 3753* (DUKE, NY), *3757* (DUKE, F, MO, NY). Las Nubes, 1900–2200 m, *Luteyn 3811* (DUKE, NY). E slopes of Cerro Horqueta, 1700–1800 m, *Luteyn & Wilbur 4605* (DUKE, MO). Cerro Colorado cloud forest along continental divide, 1200–1500 m, *Mori & Dressler 7765, 7887* (both MO, NY). Palo Alto just E of Boquete, 1540 m, *Stern et al. 1069* (GH, MO, US). E slopes of Cerro Horqueta, 1700–1800 m, *Wilbur & Luteyn 19206* (DUKE). Trail along upper Río Chiriquí Viejo, 2 km N of Cerro Punta, *Wilbur et al. 13087, 15373* (both DUKE, MO). Bajo Mono and Quebrada Chiquero, 1500 m, *Woodson & Schery 574* (GH, NY), *576* (MO). Bajo Chorro, 1900 m, *Woodson & Schery 632* (GH, MO, NY). COCLÉ: Trail to La Mesa N of El Valle, 1000 m, *Allen 2721* (A, F, MICH, MO, NY, UC, US). N of El Valle, *Allen 3637* (G, GH, MO, NY, S, US). La Mesa, 810 m, *Croat 25330* (MO); *D'Arcy & D'Arcy 6761* (MO). Between Cerro Pilón and El Valle de Antón, 700–900 m, *Duke & Dwyer 13937, 13959* (both MO, UC). Cerro Pilón, 1000 m, *Dwyer & Lallathin 8609A* (NY). Trail to Los Llano beyond La Mesa, 800–860 m, *Luteyn 3169* (DUKE). Trail beyond La Mesa to the E, *Luteyn & Kennedy 1729* (DUKE, F, MO, NY, PMA). DARIÉN: Serrania de Pirre, 9–10 km N of Alto de Nique, 1520–1560 m, *Croat 37869* (MO, NY). Serrania de Pirre, along headwaters of Río Escucho Ruido, ca. 16 km N of Alto de Nique, 1530–1550 m, *Croat 37927* (MO, NY). Cerro Pirre, *Bristan 604(2)* (MO); *Duke 6079* (MO). PANAMÁ: Cartí-El Llano-Tupile road, 15–16 km beyond Interamerican Highway, 400 m, *Busey 365* (DUKE). Campo Tres, beyond Cerro Jefe, 500–800 m, *Croat 27063* (MO). Cerro Jefe, *Duke 8017(2)* (MO). Cartí-El Llano-Tupile road, 15–16 km beyond Interamerican Highway, 400 m, *Kennedy et al. 2409* (MO). 12 mi above Pan American Highway, along the Cartí-Tupile road, 200–500 m, *Liesner 684* (MO). Campo Tres, beyond Cerro Jefe, 500–800 m, *Liesner 549* (MO); Cartí-El Llano-Tupile road, 10–12 km N of Interamerican Highway, 500 m, *Luteyn & Wilbur 4680* (DUKE, MO). El Llano-Cartí road, 12.7 km from Inter-American Highway, *Mori et al. 4692* (NY). El Llano-Cartí road, 16–18 km above Inter-American Highway, *Nee & Tyson 10956* (NY). El Llano-Cartí road, 8–12 km N of El Llano, *Nee et al. 8745* (NY). Cerro Jefe, trail leading from summit W, *Witherspoon & Witherspoon 8493* (MO, NY); Cerro Jefe, summit area, *Witherspoon et al. 8281* (MO, NY). VERAGUAS: Road between Escuela Agrícola Alto Piedra and Calóvebora, 350–400 m, *Croat 27394* (MO). Road beyond the Escuela Agrícola Alto Piedra, 800–1000 m, *Luteyn & Wilbur 4573* (DUKE, MO, NY). 8.8 km from Escuela Agrícola Alto Piedra, NW of Santa Fé, *Mori & Kallunki 3213* (NY). First branch of the Río Santa María, NW from Santa Fé, *Witherspoon & Dressler 8920* (MO, NY).

6. **Cavendishia chiriquiensis** A. C. Smith, Ann. Missouri Bot. Gard. 28: 449. 1941. TYPE: Panama; *Woodson & Schery 688* (NY, holotype; photo of holotype, DUKE, NY; MO, isotype).

Weakly erect, epiphytic *shrub* to 3 m tall, the stem base ca. 3 cm in diameter; mature branches terete, smooth to minutely striate, glabrous, tan, grayish red or reddish brown; immature branches and the twigs of the new growth terete to bluntly angled, smooth or striate, glabrous, tan, infrequently with caducous, globular glands on the recent growth. *Leaves* elliptic, 4.5–8 cm long, 1.5–3.5 cm wide, basally cuneate or sometimes attenuate, apically caudate acuminate, the acumen 1.5–2(–2.5) cm long, averaging ¼–⅓ of the total leaf length, brownish to grayish green or tan when dry, glabrous or slightly puberulous at the base of the midrib when young, glabrescent; 3–5-plinerved, the midrib, the lateral nerves, and the veinlets impressed to slightly elevated and conspicuous above, all the veins raised beneath but usually only the midrib conspicuous, newly unfolding leaves often densely provided with caducous, globular glands on the upper surface and reddish glandular fimbriate beneath; petioles terete to subterete, sometimes flattened adaxially, rugose, 4–8 mm long, 1–1.5 mm in diameter, densely white puberulous when young becoming glabrate, tan to reddish brown. *Inflorescence* viscid, 6–9(–11)-flowered, the rachis complanate, bluntly angled, sometimes flexuous, smooth or minutely striate, glabrous, 1.5–4.5 cm long, ca. 1 mm in diameter at the base, pale green suffused with red when fresh but drying brick red, infrequently with a few scattered globular glands; floral bracts glabrous, slightly ribbed, smooth, rugose or muricate, oblong to oblanceolate, basally narrowed and truncate, apically acute or rounded, 15–25 mm long, 5–9 mm broad, red, each margin with 11–12, sessile, globular glands to 0.5 mm in diameter, these often caducous; pedicels terete to angled, swollen at both ends, minutely striate, glabrous, 4–7 mm long, 0.5–1 mm in diameter, pale green when fresh but drying brick red, provided with few scattered globular glands and cilia, especially distally; bracteoles linear to linear lanceolate, 1–2(–4) mm long, ca. 0.5 mm broad, with a hastate, callose thickened, apical gland which breaks off easily, a few globular glands at the margin. *Flowers* with the calyx glabrous, 3.5–4.5 mm long, pink at anthesis, the tube cylindric, smooth or rugose, 1.5–2(–2.5) mm long, 2–3.5 mm wide, basally slightly expanded, the expansion most noticeable in the early fruit, with numerous, scattered, globular glands not obscuring the surface of the tube, the limb campanulate to erect-spreading, rugose, ribbed, 1.5–2.5 mm long, with a few scattered glands similar to those of the tube, the lobes triangular, obtuse, 0.5–1 mm long, ca. 0.5 mm wide, erect after anthesis, completely or only marginally callose thickened but appearing almost completely callose thickened because of small size of the lobes, the lobes often breaking off with age, the sinuses broadly rounded or flat; corolla 16–24 mm long, 4–4.5 mm in diameter, reddish purple at the very base, purple above, the distal ⅓ short pilose, the lobes triangular, obtuse, ca. 2 mm long; stamens 14.5–21 mm long, the filaments densely short pilose or glabrate, alternately 3 mm and 5–7.5 mm long, white, the anthers including tubules alternately 9.5–16.5 mm and 13–20 mm long, purplish orange, the thecae 3–6.5 mm long; style 17–23 mm long. *Berry* not seen.

Cavendishia chiriquiensis is endemic to western Panama and is most closely related to *C. panamensis*. Its distinctive characters are mentioned in the discussion of *C. panamensis*.

BOCAS DEL TORO-CHIRIQUÍ border: Chiriquí Trail, elfin forest at divide, *Kirkbride & Duke 979* (MO, NY). CHIRIQUÍ: Boquete region, *Hagen & Hagen 2033* (A, NY). Between Pinola and Divide, Chiriquicito-Caldera Trail, *Kirkbride & Duke 849* (MO, NY). Slopes E of Cerro Horqueta, 1800–1900 m, *Luteyn & Wilbur 4612* (BM, CAS, CR, DUKE, F, FSU, G, GH, K, LL, MICH, MO, MSU, NY, PMA, UC, US, WIS), *4617* (CAS, DUKE, F, GH, LL, MICH, MO, MSU, NY, UC, US). Cerro Colorado cloud forest on continental divide, 1200–1500 m, *Mori & Dressler 7786* (MO, NY). Slopes E of Cerro Horqueta, 1700–1900 m, *Wilbur & Luteyn 19323* (DUKE). Bajo Chorro, 1900 m, *Woodson & Schery 688* (MO, NY).

7. **Cavendishia complectens** Hemsl., Biol. Centr. Amer., Bot. 2: 272. 1881. TYPE: Costa Rica, *Endres 257* (K, holotype; photo of holotype, DUKE, NY; W, isotype).

Epiphytic and terrestrial *shrubs*, 1–1.5 m tall, glabrous throughout; stem base to about 3 cm in diameter; mature branch erect or pendent, terete to bluntly angled; bark grayish to reddish brown. *Leaves* usually subsessile, amplexicaul, drying olive brown or dark green, oval to semiorbicular, (5–)8–16(–18) cm long, (4–)5.5–10(–13) cm wide, basally cordate with the basal lobes rounded, usually imbricate, apically obtuse to broadly rounded, rarely bluntly cuspidate; pinnately veined, the midrib impressed above, raised and conspicuous beneath, lateral nerves usually raised on both the surfaces, anastomosing to form a weak, collective marginal nerve, the veinlets slightly raised and obscure to conspicuous; petioles subterete, rugose, to 5 mm long. *Inflorescence* 1(–3) rachises per axil, the largest rachis rarely once branched at the base, 10–27(–60)-flowered, the rachis terete to bluntly angled, swollen at each floral node, 2–9(–20) cm long and 1–2 mm in diameter at anthesis, increasing to 3 mm diameter postanthesis, pinkish green at anthesis, later turning purplish; floral bracts smooth or becoming ribbed after drying, elliptic to ovate lanceolate, rarely suborbicular, basally narrowed and somewhat auriculate, apically acute, (10–)11–16(–20) mm long, (5–)7–10(–17) mm wide, dark pink to red, marginally scarious and glandular fimbriate, ascending at anthesis but later spreading or perpendicular to the rachis; pedicels minutely striate or rugose, (2–)4–9(–11) mm long, 0.5–1 mm in diameter, pinkish green at anthesis but later turning purplish; bracteoles oblong to lanceolate, (1–)3–4(–7) mm long, (0.5–)1–2.5 (–4) mm wide, basally slightly auriculate, apically rounded, marginally glandular fimbriate, dark pink. *Flowers* with the calyx (4.5–)6–8(–10) mm long, the tube hemispheric, basally not enlarged, smooth or minutely muricate, (1.5–)2–3.5(–6.5) mm long, 2.5–6 mm in diameter, purplish green, the limb campanulate, coriaceous, (2.5–)4–5(–5.5) mm long including the lobes, pale green, the lobes reniform, broadly ovate, rarely oblong, imbricate, (1.5–)2–3(–4) mm long, (1.5–)3(–4.5) mm broad, glandular fimbriate, whitish green, flaring at anthesis, later connivent and tightly curling around the base of the style; corolla cylindric or bottle-shaped, narrowed at the throat, (7–)8–10(–12) mm long, 4–6.5 mm in diameter at the widest part, white at the base, purplish black in the basal ¼, the midsection green, the limb white, the lobes oblong, obtuse, 2–2.5 mm long, white;

stamens 7–8.5 mm long, the filaments white, alternately 2–3 mm and 3.5–4 mm long, with a few scattered distal hairs, the anthers orange including tubules alternately 4.5–6.5 mm and 5.5–7 mm long, the thecae 2–4 mm long; style 7–8.5 mm long, distally flaring. *Berry* 9 mm in diameter.

Cavendishia complectens is one of the easiest species to recognize because of its cordate, amplexicaul leaves. It has been collected a few times in eastern Darién Province, Panama, and in Chocó, Colombia, but is to be expected from western Panama also. It is common in the mountains of the Central Valley of Costa Rica and occurs rarely in Nicaragua.

DARIÉN: Cerro Pirre, *Bristan 596*; *Duke 5321*, *6103* (all MO). Serrania de Pirre, headwaters of Río Escucho Ruido, ca. 16 km N of Alto de Nique, 1530–1550 m, *Croat 37936* (NY). W slope of Cerro Pirre, 1000 m, *Duke 6595* (MO). Cerro Campamiento, *Duke 15728(1)* (MO). Cerro Pirre, 770–1380 m, *Duke & Elias 12751* (F, MO, NY). Cuasi-Caná Trail on Cerro Campamiento, *Kirkbride & Duke 1224* (MO, NY). Causi-Caná Trail between Cerro Campamiento and La Escalera, *Kirkbride & Duke 1339* (MO, NY). N slopes of Cerro Pirre, 700–950 m, *Mori & Kallunki 5465* (NY). Crest of Cuasi-Caná Trail, 1690 m, *Terry & Terry 1577* (A, F, MO).

8. **Cavendishia crassifolia** (Benth.) Hemsl., Biol. Centr. Amer., Bot. 2: 273. 1881.

Thibaudia crassifolia Benth., Pl. Hartw. 65. 1840. TYPE: Mexico; Oaxaca, *Hartweg 477* (K, holotype; photo of holotype DUKE, NY; FI, G, LD, LE, M, NY, US—fragments; W, isotypes).

T. mexicana Martens & Galeotti, Bull. Acad. Roy. Sci. Bruxelles 9(2): 530. 1842. TYPE: Mexico; Oaxaca, *Galeotti 1813* (BR, holotype; photo of holotype DUKE, NY).

Proclesia veraguensis Klotzsch, Linnaea 24: 35. 1851. TYPE: Costa Rica; *Warszewicz* (B, holotype not seen, presumably destroyed photo of type, DUKE, NY).

Polyboea crassifolia (Benth.) Klotzsch, Linnaea 24: 31. 1851.

Cavendishia latifolia Hemsl., Biol. Centr. Amer., Bot. 2: 273. 1881. TYPE: Mexico; Chiapas, *Linden 390* (K, holotype; photo of type DUKE, NY; F—fragments; G, isotypes).

C. veraguensis (Klotzsch) Hemsl., Biol. Centr. Amer., Bot. 2: 273. 1881.

Chupalon crassifolium (Benth.) Kuntze, Rev. Gen. Pl. 2: 383. 1891.

C. latifolium (Hemsl.) Kuntze, Rev. Gen. Pl. 2: 383. 1891.

Cavendishia guatemalensis Loesener, Bull. Herb. Boissier II. 3: 221. 1903. TYPE: Guatemala; Huehuetenango, *Seler 3107* (B, holotype not seen, presumably destroyed; photo of type, DUKE, NY; GH, NY, US, isotypes).

C. smithii Hoerold, Bot. Jahrb. Syst. 42: 328. 1909. TYPE: Costa Rica, Cartago, Volcán Irazú, *Donnell Smith 4876* (B, holotype not seen, presumably destroyed, photo of holotype DUKE NY; GH, US, isotypes).

C. costaricensis Hoerold, Bot. Jahrb. Syst. 42: 326. 1909. TYPE: Costa Rica; San José, La Palma, *Wercklé 54* (B, holotype not seen, presumably destroyed, photo of type DUKE, NY, US; NY—fragments, isotype).

C. hoffmannii Hoerold, Bot. Jahrb. Syst. 42: 328. 1909. TYPE: Costa Rica; Cartago, Volcán Irazú, *Hoffmann 141* (B, holotype not seen, presumably destroyed, photo and fragments of holotype, NY; photo of holotype DUKE).

C. chiapensis Brandegee, Univ. Calif. Publ. Bot. 6: 188. 1915. TYPE: Mexico; Chiapas, *Purpus 7342* (UC, holotype; photo of type DUKE, NY; F, GH, MO, NY, US, isotypes).

C. skutchii A. C. Smith, J. Wash. Acad. Sci. 27(7): 308. 1937. TYPE: Costa Rica; San José, El General, *Skutch 2802* (US, holotype, photo of holotype, DUKE, NY; GH, MICH, NY—fragment, S, isotypes).

C. calycina A. C. Smith, Ann. Missouri Bot. Gard. 28: 447. 1941. TYPE: Panama; Chiriquí, Boquete, *Davidson 157* (A, holotype; photo of holotype DUKE, NY).

C. guatemalensis var. *chiapensis* (Brandegee) L. O. Williams, Fieldiana Bot. 31: 169. 1965.

Epiphytic and terrestrial *shrubs*, 1–3 m tall, rarely arborescent and to 10 m tall with stem bases to 20 cm in diameter; mature branches terete or subterete,

smooth or striate, glabrous; bark brown to grayish brown; immature branches and twigs of the new growth subterete or bluntly angled, striate or ribbed, glabrous to densely pubescent, green or often red above and green beneath. *Leaves* oblong, elliptic, ovate or lanceolate, rarely oblanceolate or semiorbicular, 4–15(–22) cm long, 1.5–5(–11) cm wide, basally rounded, cuneate, subcordate, subtruncate or rarely short attenuate, apically acute to acuminate, often abruptly so and rarely rounded or cuspidate, green, olive green or brownish, sometimes metallic or slate blue when dry, glabrous or short pilose along the veins above and below; (3–)5–7(–9)-plinerved, innermost lateral nerves sometimes rising 1–2 cm above the base, midrib impressed above and raised beneath, always conspicuous, sometimes flattened adaxially, lateral nerves impressed or slightly raised distally above, raised beneath, the veinlets impressed or raised above, slightly raised but usually obscure beneath; petioles subterete, usually flattened adaxially, rugose, (3–)5–11(–17) mm long, 1–4 mm in diameter, glabrous, puberulent or pilose, reddish brown when dry. *Inflorescence* (4–)6–20(–40)-flowered, encircled at the base by bracts, the bracts glabrous to densely short pubescent, the pubescence often restricted to the margins or the apex, the rachis subterete to bluntly angled, (0.5–)1–5(–8) cm long, green or red, glabrous or pubescent with short white trichomes; floral bracts smooth or muricate, glabrous to densely short pilose, sometimes pubescent only along the margins or distally, oblong, ovate, elliptic to oblanceolate, basally narrowed and truncate, apically rounded or acute, (11–)17–26(–40) mm long, (5–)10–17(–27) mm wide, pink to dark red, sometimes provided with reddish, glandular fimbriae abaxially; pedicels often swollen distally, striate or ribbed, sometimes rugose, (3–)6–15(–20) mm long, 1–3 mm in diameter, pale green to dark rose red, glabrous or pilose, often with glandular fimbriae scattered along the length or densely aggregated distally; bracteoles oblong, ovate, lanceolate, linear lanceolate, rarely aristate, 1–4(–8) mm long, 0.5–2(–5) mm broad, glabrous to densely glandular fimbriate, sometimes ciliate. *Flowers* with the calyx glabrous to densely short pilose, (3.5–)4–6(–10.5) mm long, pale green to red, usually with few to many short, stout, glandular fimbriae, the tube cylindric, smooth or somewhat rugose, often somewhat pentagonal in cross section, 1.5–3(–4) mm long, not basally enlarged, the base often rounded or truncate and shallowly undulate, the limb cylindric to campanulate, usually somewhat spreading, (1.5–)2–3(–6) mm long including the lobes, the lobes triangular, rarely oblong, (0.5–)1–2(–5) mm long, connivent after anthesis, marginally glandular fimbriate, sinuses broadly rounded or acute; corolla cylindric to bottle-shaped, narrowed to the throat, (12–)15–20(–25) mm long, 4–5 mm in diameter, glabrous to short pilose, with or without scattered glandular fimbriae, pale pinkish to white at the base, the tube otherwise dark pink to red, the limb and the lobes white, the lobes deltoid, widely flaring at anthesis, 1–2 mm long; stamens 11.5–19 mm long, the filaments distinct or slightly coherent at the base, glabrous or distally pubescent, alternately 2–4 mm and 3.5–6.5 mm long, white or pinkish white, the anthers including the tubules alternately 7.5–14.5 mm and 10–16.5 mm long, yellow to orange, the thecae 2.5–6 mm long; style glabrous or rarely distally short pilose, (12–)14–19(–27) mm long. *Berries* 8–14 mm in diameter.

Cavendishia crassifolia is the most frequently encountered species of *Cavendishia* in southern Mexico and throughout montane Central America. It is recognized as a complex of wide-ranging, variable populations. Previous authorities have subdivided the complex into no fewer than 11 species. All of these species were described from single collections, from different geographical areas, and were based upon characters now seen to be unstable. The floral characters of the populations within this complex are virtually identical. Although there are local differences across the geographical range, there are no consistent morphological types associated with realistic geographical ranges, nor are there discontinuities in any combination of characters which could result in a meaningful subdivision. The complex also seems to range into South America where similar problems are to be expected.

Although specimens from the vicinity of Volcán Chiriquí were identified as *C. miconioides* by A. C. Smith, comparisons of the more numerous collections now available show these populations to be local variants of *C. crassifolia.*

BOCAS DEL TORO: Chiriquí Trail between Criollo and Quebrada Hondo, *Kirkbride & Duke 793* (NY). Róbalo Trail, N slopes of Cerro Horqueta, 1840–2160 m, *Allen 4934* (G, MO, US). CHIRIQUÍ: Llanos area NE of El Hato del Volcán, *Allen 1539* (MO); *Allen & Fairchild 3463* (F, G, GH, MO, NY, S, US). S of Finca Lerida, 1840–2160 m, *Allen 4771* (F, G, MO, US). Summit and SW face of Cerro Copete, 2770 m, *Allen 4891* (F, G, GH, MO, US), *4893* (BM, BR, G, MO, US). Boquete, 1500 m, *Maurice 718* (US). Llanos area NE of El Hato del Volcán, *Correa & Lazor 1399* (DUKE). Slopes of Las Cumbres near Cerro Punta, *Croat 13756* (MO); *Croat & Porter 16068* (MO). Between Boquete and Monte Rey, *Croat 15629* (MO). 2.2 km SW of Cerro Punta on road above IDAAN water tank, 2100–2250 m, *Croat 26300* (MO, NY). Above San Félix along mining road, 17–18 mi off Panamerican Highway, 1200–1500 m, *Croat 33096* (MO, NY). Above San Félix along mining road 18–27 mi off Panamerican Highway, 1200–1500 m, *Croat 33113* (NY). E slope of Volcán Barú, 2400 m, *Davidse & D'Arcy 10220* (NY). Llanos area NE of El Hato del Volcán, *Davidse & D'Arcy 10369* (NY). W slope of El Barú, 2160–2460 m, *Davidse & D'Arcy 10261* (NY). Bajo Chorro, 1840 m, *Davidson 157* (MO), *343* (F). Volcán Chiriquí, Boquete District, 2770 m, *Davidson 973* (DS, MO, US). Chiriquicito-Caldera Trail between Pinola and Divide, *Kirkbride & Duke 842A* (MO). Chiriquí Trail between Pinola and Quebrada Hondo, *Kirkbride & Duke 911* (MO, NY). Chiriquí Trail between Quebrada Hondo and Divide, *Kirkbride & Duke 924* (NY). Las Nubes, NW side of Cerro Punta, 2200–2300 m, *Luteyn 3043* (DUKE, MO). Bajo Chorro, summit, 2200–2210 m, *Luteyn 3046* (DUKE, F, MO, NY). Llanos area NE of El Hato del Volcán, *Luteyn 3049* (CAS, DUKE, F, FSU, GH, LL, MICH, MO, MSU, NY, PMA, UC, US, WIS). Cerro Horqueta, 1800–1900 m, *Luteyn 3079* (DUKE, MO). Bajo Mono Trail, NW of San Ramón, 1600–1700 m, *Luteyn 3729* (DUKE, F, MO, NY); *Luteyn 3741* (DUKE). Las Nubes vicinity, NW side of Cerro Punta, 2200–2300 m, *Luteyn 3800* (DUKE). Bajo Chorro, 2360–2500 m, *Luteyn 3835* (DUKE). Las Nubes vicinity, NW side of Cerro Punta, 2200–2300 m, *Luteyn & Wilbur 4639* (DUKE, MO). Cerro Colorado, cloud forest along divide, 1200–1500 m, *Mori & Kallunki 5883, 5894* (both NY); *Mori & Dressler 7860* (MO, NY). Cerro Pando, on continental divide and Panama-Costa Rican border, ca. 16 km NW of El Hato, 2000–2482 m, *Mori & Bolten 7289* (MO, NY). W side Volcán Barú, oak forest, 2000–2500 m, *Mori & Bolten 7357* (MO, NY). Llanos area NE of El Hato del Volcán, *Seibert 321* (MO). Finca Collins near Boquete, *Sullivan 401* (FSU). Deep arid canyon, 5 mi NE of El Volcán, 1935–2000 m, *Tyson 807* (FSU, MO). Dry windswept canyon, 8 mi NE of El Hato, 2500–2580 m, *Tyson 830* (FSU), *840* (FSU, MO). Deep arid canyon, 5 mi NE El Volcán, 2160 m, *Tyson 6343* (FSU, MO). W slope of El Barú, 1840–2160 m, *Tyson & Loftin 5944* (DUKE, FSU, MO). W slope of El Barú, 2160–2460 m, *Tyson & Loftin 5995* (DUKE, FSU, MO). W slope of El Barú, 2460–2770 m, *Tyson & Loftin 6115* (DUKE, FSU). Valley of upper Río Chiriquí Viejo, 1300–1900 m, *White & White 35* (MO, NY). Lava fields NE of El Hato near Aguacate, 1800–1900 m, *Wilbur et al. 10969* (CAS, DUKE, F, GH, MICH, MO, NY); *Wilbur et al. 10974* (DUKE, F, MO). Lava fields 4 mi NW of El Hato near Río Macho de Monte, 1800 m, *Wilbur & Teeri 13076* (DUKE, F, MO). Las Nubes vicinity, NW of Cerro Punta, 2200–2300 m, *Wilbur & Teeri 13206* (DUKE); *Wilbur & Teeri*

13222 (DUKE, F, GH, MO). Lava field and slopes beyond Volcán Chiriquí and Cerro Aguacate, 2000–2200 m, *Wilbur & Teeri 13326* (BM, CAS, CR, DUKE, F, FSU, G, GH, K, LL, MICH, MO, MSU, NY, PMA, UC, US, WIS). Southern slopes of Cerro Horqueta, 2210 m, *Wilbur et al. 13484* (DUKE, MO, NY), *17301* (DUKE). Llanos area NE of El Hato del Volcán, *Wilbur et al. 15406* (BM, CAS, CR, DUKE, F, FSU, G, GH, K, LL, MICH, MO, MSU, NY, PMA, UC, US, WIS). Casita Alta to Cerro Copete, 2300–3300 m, *Woodson & Schery 357* (GH, MO, NY). COCLÉ: Cerro Caracoral, elfin forests, *Duke & Dwyer 15117(2)* (NY); *Kirkbride 1101* (MO, NY). VERAGUAS: Vicinity of Santa Fé, slopes of Cerro Tute, 925–1000 m, *Allen 4340* (F, G, GH, MO, NY, US); *Mori 6757* (NY). Trail up E side of Cerro Tute, to 1200 m, *Witherspoon & Dressler 8845* (MO, NY).

9. **Cavendishia darienensis** Luteyn, Brittonia 28: 43. 1976. TYPE: Panama; Darién, Río Balsa, between Manene and Aretí, *Duke 13509(6)* (US, holotype, photo of holotype DUKE, NY; WIS, isotype).

Terrestrial and epiphytic *shrubs*, mature branches terete to subterete, slightly angled, minutely striate, glabrous, reddish to grayish brown when dry; immature branches and twigs of new growth subterete, ribbed, striate, densely short pilose or glabrous. *Leaves* oblong to oblong elliptic, 5.5–10 cm long, 2.5–4.5 cm wide, basally subcordate, apically obtuse, glabrous or with scattered, short trichomes along the base of the midrib and the lateral nerves, the margins of the young leaves often short pilose; 5-plinerved, the midrib and the lateral nerves strongly impressed proximally, plane to slightly elevated above distally, raised and conspicuous beneath and the leaves then bullate, the veinlets raised and conspicuous above, slightly raised but obscure beneath; petioles subterete, bluntly angled, rugose, 4–6 mm long, 1.5–2 mm in diameter, densely puberulent becoming glabrous. *Inflorescence* 26–28-flowered with the lowest few (up to 5) nodes sterile, encircled at the base by puberulent, ovate, apiculate bracts; rachis bluntly angled, striate, densely short pilose, 8.5–9.5 cm long, 2–2.5 mm in diameter; floral bracts prominently striate on both the surfaces with conspicuous midrib, lanceolate, (14.5–)18.5–23 mm long, 6–9 mm wide, basally cuneate and strongly concave, apically long acuminate, marginally glandular fimbriate, densely short hirsute on both the surfaces with white trichomes 0.2–0.4 mm long, pink (according to label data); pedicels subterete, 1–2.5 mm long, 0.5–1 mm in diameter, short white pilose; bracteoles lanceolate, apically long acuminate, striate, (8–)13–16 mm long, 3.5–4.5(–6.5) mm broad, marginally glandular fimbriate, densely short pilose as the floral bract, clasping the base of the calyx, slightly spreading distally. *Flowers* with the calyx 7–9.5 mm long, abruptly widened at the junction of the tube and the limb, short pilose from the base of the tube to the tip of the lobes, the tube smooth, subglobose, slightly rugose, basally rounded, 2–2.5 mm long, the limb cylindric to slightly spreading, conspicuously striate as the lobes, 5.5–7 mm long including the lobes, the lobes long triangular, 2–4 mm long, 2–2.5 mm wide, erect after anthesis, marginally scarious and eglandular, pubescent within; sinuses obtuse; corolla bluntly 5-angled opposite the calyx sinus, densely short pilose without, glabrous within and at the base where surrounded by calyx limb, 11.5 mm long, 3–3.5 mm in diameter, with scattered, short, red, clavate fimbriae on the surface, the lobes obtuse, erect; stamens alternately 8–8.5 mm and 8.5–9 mm long, the filaments weakly short pubescent distally, alternately 2–2.5 mm and 3.5–4 mm long, the

anthers alternately either 6–6.2 mm or 6.5–7 mm long, the thecae 2–2.5 mm long; style 9.5–10.5 mm long. *Berry* not seen.

Cavendishia darienensis is found in Darién, Panama and adjacent Chocó, Colombia at 100–950 m elevation. Is is most closely allied to *C. allenii*, another lowland species but endemic to central Panama. The two species share similar gland types on the calyx lobes and bracteoles, and in addition, both possess prominently nerved or striate floral bracts, bracteoles and calyces.

DARIÉN: Between upper Río Membrillo and Camp 7 on the construction road to San Blas, *Duke 10888(2)* (MO). Río Balsa, between Manene and Aretí, *Duke 13509* (MO, US, WIS). Cerro Pirre, *Mori & Kallunki 5483* (MO, NY).

10. **Cavendishia fusiformis** Luteyn, Brittonia 28: 42. 1976. TYPE: Panama, *Kirkbride & Duke 1276* (MO, holotype; photo of holotype, DUKE, NY; NY, isotype).

Epiphytic *shrub*; immature branches and twigs of the new growth terete, somewhat rugose, moderately hirsute or glabrate, trichomes 1–2 mm long, tan to tawny yellow. *Leaves* elliptic or oblong elliptic, (4.5–)9–14 cm long, (1–)2–4 (–6) cm wide, basally narrowing and obtuse, apically acuminate, grayish or brownish green above and tan beneath when dry, sparsely short pilose along the nerves above, moderately pilose or glabrate beneath with tawny yellow trichomes; 3(–5)-plinerved, the midrib weakly impressed or plane above, raised and prominent beneath, the lateral nerves weakly impressed or more commonly elevated on both the surfaces as the veinlets; petioles terete or infrequently flattened adaxially, rugose, 4–7 mm long, 2 mm in diameter, hirsute. *Inflorescence* obconic or fusiform at anthesis, ca. 20-flowered, the lowest nodes sterile, circumscribed at the base by striate bracts; rachis glabrous, smooth, fusiform, 3–8 cm long, 5–6 mm in diameter medially, the nodes congested; floral bracts glabrous, striate, marginally scarious, oblong obovate, basally narrowing and rounded, apically rounded and emarginate, commonly tearing, 25–35 mm long, 13–18 mm wide, red to rose pink, with subsessile, capitate, red glands located at the base; pedicels subterete, glabrous, ca. 1 mm long, 1–1.5 mm in diameter; bracteoles oblong or oblanceolate, imbricate, basally clasping the calyx, apically rounded and shallowly emarginate, 25–30 mm long, ca. 10 mm broad, with subsessile, capitate, red glands as on the floral bracts. *Flowers* with the calyx glabrous, 11–15 mm long, the tube barrel-shaped, smooth, 2.5–4 mm long, not enlarged basally, the limb erect, spreading, submembranaceous, striate, 9–12 mm long including lobes, the lobes linear oblong, acute, 3–6 mm long, erect after anthesis, the few, stout, glandular marginal fimbriae occasionally distally fused, sinuses obtuse to broadly rounded; corolla glabrous, membranaceous basally and subcoriaceous apically, 34–35 mm long, 6–7 mm in diameter, white with green tips; stamens alternately 10–11.5 mm and 12–13.5 mm long, about ⅓ the length of the corolla, the filaments distinct or slightly coherent basally, glabrous, alternately 1–2 mm and 3.5–4.5 mm long, the long filaments conspicuously narrowed and thin distally, the anthers including the tubules alternately 8–9 mm and 9–10.5 mm long, the thecae smooth, 2.5–3 mm long, the tubules dehiscing by

short, oblique pores or oval clefts 1–1.5 mm long; style 33–37 mm long. *Berry* not seen.

Cavendishia fusiformis is endemic to eastern Darién Province. It is closely related to a group of Colombian species described by A. C. Smith; *C. glandulosa*, *C. venosa*, *C. speciosa*, *C. micayensis*, and *C. chlamydantha*. As a group these species are unique in having stamens which are usually one-third to one-half the length of the corolla, rachises which are distinctly clavate or fusiform in shape, calyx limbs tending to be elongate and infundibuliform, and corollas which are membranaceous below and somewhat coriaceous above.

DARIÉN: Cerro Pirre, *Bristan 542(2)* (MO); *Duke 6119* (MO), *Gentry & Clewell 6952* (MO). Cañá-Cuasí Trail between Cerro Campamiento and La Escalera to "páramo," E of Tres Bocas, *Kirkbride & Duke 1276* (DUKE, MO, NY). Cerro de Garagára, Sambú basin, 500–974 m, *Pittier 5651* (US). Cana-Cuasí Trail, 1690 m, *Terry & Terry 1567* (A, F, MO).

11. **Cavendishia gentryi** Luteyn, Brittonia 28: 400. 1976. TYPE: Panama; Darién, Cerro Tacarcuna, *Gentry & Mori 13971* (MO, holotype; photo of holotype, NY; DUKE, NY, isotypes).

Epiphytic *shrub*, mature branches terete, smooth, glabrate, brown; immature branches and twigs of the new growth terete, smooth, reddish brown, densely pilose with white hairs to 4 mm long. *Leaves* elliptic to ovate elliptic, 8–13 cm long, 3.5–5.5 cm wide, basally rounded, apically abruptly acuminate, brownish green when dry, densely pilose beneath with hairs to 2 mm long, scattered pilose above; 3(–5)-plinerved, the midrib, the lateral nerves and the primary veins impressed and conspicuous above, elevated beneath, the veinlets slightly elevated above, obscure beneath; petioles terete, rugose, 5 mm long, 2 mm diameter, densely pilose with tan hairs to 3 mm long. *Inflorescence* short racemose, 6-flowered; rachis terete, striate, densely pilose, ca. 2.5 cm long; floral bracts lanceolate, long acuminate, 16–23 mm long, 4–6 mm wide, densely pilose marginally, scattered pilose on the lamina, trichomes to 2 mm long; pedicels swollen distally, striate, densely pilose, 8–12 mm long; bracteoles not seen. *Flowers* with the calyx densely pilose, 13–13.5 mm long, pink, the tube spherical, 3.5–4.5 mm long and broad, not expanded, the limb short cylindric or somewhat spreading, 9–9.5 mm long including the lobes, the lobes linear lanceolate, acute, 8 mm long, ca. 2 mm broad at the base, erect after anthesis, marginally with 3–4 gland-tipped fimbriae on each side, sinuses acute; corolla (past anthesis) cylindric, ca. 20 mm long, scattered pilose with the hairs denser at the lobe tips; stamens ca. 16 mm long, the filaments alternately ca. 1 mm and 3 mm long, the anthers including tubules alternately ca. 15 mm and 13 mm long, the thecae 3–4 mm long; style ca. 21 mm long. *Berry* not seen.

Cavendishia gentryi, endemic to Darién Province, is most closely related to *C. darienensis*. The two species are easily separated however, by the leaf shape and by the shorter rachis with fewer flowers, the nonstriate floral bracts, longer pedicels, more densely pilose calyx, and glandular calyx lobes of *C. gentryi*.

DARIÉN: Cerro Tacarcuna, elfin forest at top of W peak, 1800–1850 m, *Gentry & Mori 13971* (DUKE, MO, NY).

12. **Cavendishia laurifolia** (Klotzsch) Benth. & Hook., Gen. Pl. 2: 570. 1876.

Polyboea laurifolia Klotzsch, Linnaea 24: 31. 1851. TYPE: Guatemala; Alta Verapaz, *Warszewicz* (B, lectotype, not seen, presumably destroyed; photo of lectotype, DUKE, F, NY).
Chupalon laurifolium (Kl.) Kuntze, Rev. Gen. Pl. 2: 383. 1891.
Cavendishia tuerckheimii Hoerold, Bot. Jahrb. Syst. 42: 323. 1909. TYPE: Guatemala; Alta Verapaz, Cobán, *Tuerckheim 64* (B, holotype, not seen, presumably destroyed, photo of type DUKE, NY; GH, NY, US, isotypes).

Epiphytic or terrestrial *shrubs*, 1–3 m tall; stem base 2.5–5 cm in diameter; mature branches arching, terete, striate, glabrous; bark tan to grayish brown; immature branches and twigs of the new growth subterete or flattened with blunt angles, striate, reddish brown, densely puberulous and often with short, reddish, glandular fimbriae. *Leaves* slightly bullate when fresh, drying bullate or flat, lanceolate, ovate or lance elliptic, (3.5–)6–12.5 cm long, (1–)2–4 cm wide, basally rounded or obtuse, rarely subcordate, apically acuminate, tan or olive brown when dry, puberulous above along the proximal portions of the midrib and the lateral nerves, glabrous beneath; 3–5-plinerved, the midrib and the lateral nerves impressed above, the veinlets raised and conspicuous above, the midrib and the lateral nerves raised and conspicuous beneath, veinlets plane or raised but obscure beneath; petioles subterete, smooth, striate, or commonly rugose, 2–5 mm long, 0.5–1.5 mm in diameter, densely puberulous adaxially, reddish brown. *Inflorescence* (8–)17–32(–45)-flowered with the lowermost nodes bracteolate but sterile; rachis subterete, striate, weakly muricate, glabrous, 4–15(–20) cm long, 1.2 mm in diameter, rose pink at anthesis but turning whitish or pale green; floral bracts muricate, glabrous, oblong, obovate, or oblanceolate, 7–13 mm long, 3.5–6.5(–10) mm wide, basally narrowed, apically obtuse to broadly rounded, rarely acute, marginally scarious and glandular fimbriate, the bract concave, oriented perpendicular to or somewhat recurved with respect to the rachis, deep rose pink; pedicels swollen distally, striate, 10–17 mm long at anthesis, 0.5–1 mm in diameter, 10–22(–26) mm long in fruit, rose pink at anthesis but turning whitish or pale green, provided with reddish, glandular fimbriae 0.3 mm long when young, these caducous; bracteoles oblong to ovate, 1–2.5 mm long, 0.5–1(–2) mm broad, basally slightly auriculate, marginally glandular fimbriate, rose pink. *Flowers* with the calyx 2.5–3.5 mm long, green in bud, dark wine red at anthesis, later turning green, the tube cylindric but slightly pentagonal in cross section, rugose, 0.5–1 mm long, 2.5–3(–4) mm in diameter, basally slightly expanded, densely covered in bud by reddish, glandular fimbriae, the limb broadly campanulate, muricate, 1.5–3 mm long including the lobes, densely glandular fimbriate, these fimbriae usually persisting to fruit, the lobes triangular or oblong, (0.2–)0.5–1 mm long, connivent after anthesis, marginally thin and glandular fimbriate, sinuses acute in bud, becoming broadly rounded to flat at anthesis; corolla bottle-shaped, bluntly 5-angled opposite calyx lobes, constricted basally, (6.5–)8–10(–12) mm long, 5.5–6.5 mm in diameter at the widest point, the tube with scattered glandular fimbriae, white for lowest ⅔, dark rose red in the upper ⅓ plus the limb and the lobes, the lobes oblong, acute, slightly flaring at anthesis; stamens alternately either 6–7 mm or 7–8.5 mm long, the filaments densely puberulous in distal

half, alternately either 1.5–3 mm or 2.5–4 mm long, white to pinkish white, the anthers including tubules alternately 4–5.5 mm and 5.5–7 mm long, orangish brown to maroon, the thecae 1.5–3 mm long; style 8–9 mm long. *Berry* glabrous, 6–7 mm in diameter.

The three collections cited below are the first modern records of *C. laurifolia* outside its principal range of the Mexico-Guatemalan border area. Although there existed a Warszewicz collection (BR, W) which bore the label data "Costa Rica et Veragua," Luteyn (1976) doubted the credibility of this data because of other questionable Warszewicz collection sites. The recent collections from Darién however verify the presence of *C. laurifolia* in Panama.

DARIÉN: Summit of Cerro Pirre, cloud forest, 1000–1400 m, *Gentry & Clewell 7107* (DUKE, MO). Serrania del Darién, W of Unguia on Panama-Colombia border, 1150 m, *Gentry et al. 17036* (NY). W slope of Cerro Pirre, 1000 m, *Duke* 6585 (MO).

13. **Cavendishia megabracteata** Luteyn, Brittonia 28: 49. 1976. TYPE: Panama; *Luteyn & Wilbur 4594* (DUKE, holotype; F, GH, LL, MICH, MO, NY, PMA, US, isotypes).

Terrestrial or epiphytic *shrubs* to 2.5 m tall, stem base to 5 cm in diameter; mature branches terete, minutely striate, glabrous; bark brown, drying grayish to reddish brown; immature branches and twigs of the new growth terete to bluntly angled, striate, glabrous, reddish brown when dry. *Leaves* ovate, lanceolate, lance elliptic or oblong, (4–)8–12(–15) cm long, (1–)2.5–7 cm wide, basally obtuse, rounded to truncate, apically acuminate, often abruptly so, dark olive to grayish brown when dry, usually puberulous at the base of the midrib and the lateral nerves on the upper surface; 5–7-plinerved, the midrib and the inner lateral nerves moderately or weakly impressed above but sometimes plane or raised distally, the outer lateral nerves and the veinlets raised and usually conspicuous above, rarely impressed, all the nerves raised beneath but the veinlets often obscure; petioles subterete, often flattened adaxially, rugose, rarely striate, 4–10(–13) mm long, 1–2.5(–3) mm in diameter, glabrous to densely puberulent adaxially when young, often glabrate and reddish brown at maturity. *Inflorescence* (2–)5–9(–12)-flowered, often lowest one or two nodes sterile, obconic to spherical in bud; rachis coarsely and bluntly angled, striate, glabrous, (0.6–)0.8(–3.5) cm long, ca. 2 mm in diameter, cream colored and often suffused with pink when fresh, rarely with a few clavate glands or cartilaginous teeth at the base; floral bracts often translucent when dry, glabrous, smooth with minute, red, clavate, glandular fimbriae abaxially, oblong, obovate or rarely subrotund, basally narrowed and somewhat clasping, apically rounded, usually deeply emarginate (2–)3–6(–7) cm long, (1–)1.5–2.5(–4.5) cm wide, pale purplish to bright rose or dark pink when fresh; pedicels swollen distally, striate, glabrous, (8–)10–16(–19) mm long, (0.5–)1(–1.5) mm in diameter, cream colored and often suffused with pink when fresh, rarely weakly glandular at the distal end; bracteoles with or without prominent midrib, ovate, lanceolate, lance elliptic or nearly linear, 1.5–2(–5) mm long, 0.5–1.5(–4) mm wide, apically callose thickened; calyx glabrous, 7–11(–13) mm long, cream colored and often suffused with

pink, the tube cylindric, ribbed, 2–5 mm long, 3–5 mm in diameter at the base, basally enlarged and deeply lobed, the lobes straight to flaring outward and extending well below articulation, the limb cylindric to slightly spreading, smooth or minutely papillate, (4–)5–7.5(–9) mm long including the lobes, the lobes triangular, (1–)1.5–2(–2.5) mm long, erect after anthesis, the tips completely glandular callose thickened or callose thickened apically, centrally or only marginally, sinuses subacute when fresh, but drying obtuse to broadly rounded, rarely flat; corolla slightly constricted basally and at the throat, often translucent when dry, 31–40(–43) mm long, 7–9 mm in diameter, glabrous or rarely pilose distally, the tube dull or glossy white, often basally pink to pinkish below, grading through violet to pale purple above, the limb white, the lobes oblong, obtuse, 1.5–2 mm long, reflexed at anthesis, white but sometimes marginally purple; stamens 24.5–36 mm long, the filaments densely puberulous distally, alternately 2.5–7.5 mm and 7.5–13.5 mm long, white, the anthers including tubules alternately 16–26.5 mm and 21.5–32.5 mm long, yellowish to tawny orange, the thecae 6–13 mm long; style 32–41 mm long. *Berry* not seen.

Cavendishia megabracteata, endemic to western Panama, may be distinguished by the combination of large and usually emarginate floral bracts, short rachis, and few-flowered inflorescences which are obconic or spherical in bud. Both the floral bracts and the corolla are extremely thin and translucent when dry. The size, shape and texture of the floral bracts alone serve to distinguish this species from all other Mexican-Central American species of the genus.

BOCAS DEL TORO: Róbalo Trail, N slopes of Cerro Horqueta, 1840–2160 m, *Allen 4974* (G, MO, US). CHIRIQUÍ: Bajo Chorro, 1900–2500 m, *Allen 1427* (MO, US). Bajo Mono-Róbalo Trail, 1540–2160 m, *Allen 4841* (G, MO, US). Cerro Horqueta, 1700–2100 m, *Cochrane et al. 6258* (WIS). Bajo Chorro, 1900–2500 m, *Davidson 86* (F, MO). Cerro Horqueta, 1700–2100 m, *Dwyer et al. 453* (MO); *Hagen & Hagen 2034* (NY), *2047* (GH, NY), *2175* (GH, NY); *Lewis et al. 439* (DUKE, MO, SCZ); *Luteyn 3078* (DUKE, MO, NY), *3758* (CAS, DUKE, F, GH, MICH, MO, NY, US), *3789* (DUKE). Slopes E of Cerro Horqueta, 1700–2000 m, *Luteyn & Wilbur 4594* (DUKE, F, GH, LL, MICH, MO, NY, PMA, UC, US). Between Alto de Las Palmas and Cerro Horqueta, 2100–2268 m, *Maxon 5446* (US); *Pittier 3206* (F, NY, US). Cerro Hornitos, 40 km NW of Gualaca, cloud forest at 2233 m, *Mori & Boulton 7497* (MO, NY). Cerro Horqueta, Finca Collins, *Sullivan 409* (FSU). Slopes E of Cerro Horqueta, 1700–2000 m, *Wilbur & Luteyn 19227* (DUKE, MO, NY). Cerro Horqueta, 1700–2100 m, *Wilbur et al. 13458* (DUKE, F, GH, LL, MICH, MO, NY, PMA, US). Bajo Mono, 1840 m, *Wilbur et al. 13530* (DUKE, F, GH, MO, NY, US). Bajo Chorro, 1900–2500 m, *Woodson & Schery 619* (GH, MO, NY), *692* (MO).

14. **Cavendishia melastomoides** (Klotzsch) Hemsl., Biol. Centr. Am., Bot. 2: 273. 1881.

Socratesia melastomoides Klotzsch, Linnaea 24: 23. 1851. TYPE: Costa Rica, *Warszewicz* (B, holotype, not seen; photo DUKE, NY).

14a. **Cavendishia melastomoides** var. **coloradensis** Luteyn, Brittonia 28: 401. 1976. TYPE: Panama, *Mori & Dressler 7776* (NY, holotype; MO, isotype).

Epiphytic *shrub*, mature branches pendent, terete, smooth, glabrous, tan to reddish brown when dry; immature branches subterete, bluntly angled, striate, glabrous or rarely sparsely short pilose, provided with tiny, reddish,

caducous glands. *Leaves* elliptic, lanceolate, or ovate lanceolate, (3–)6–10 cm long, (2–)2.5–3.5 cm wide, basally rounded or cuneate, apically long acuminate or caudate acuminate, brownish green to tan when dry, glabrous; 3(5–)-plinerved, the midrib impressed and prominent above or somewhat plane distally, raised and conspicuous beneath, the lateral nerves slightly raised on both the surfaces or rarely impressed above, conspicuous only above; petiole subterete, flattened adaxially, rugose, (3–)4.5–9 mm long, 0.5–1.5 mm in diameter, glabrous or densely short pilose, becoming glabrate, reddish brown. *Inflorescence* usually with all parts viscid, 6–10-flowered; rachis subterete or bluntly angled, glabrous, (2–)2.5–3.5(–4.5) cm long, and 1–1.5 mm in diameter with scattered red, clavate glands; floral bracts glabrous, oblong, apically rounded, basally slightly clasping, 6–10 mm long, 3–6 mm wide; pedicels striate, ribbed, glabrous, 10–19 mm long, 0.5–1 mm in diameter, with glands as on the rachis; bracteoles strongly nerved, somewhat striate, broadly ovate to semiorbicular, apically rounded and apiculate, the apiculum callose thickened, basally auriculate, 2.5–4.5 mm long and broad. *Flowers* with the calyx glabrous, (3–)4.5–7.5 mm long, red, the tube smooth or rugose, 5-angled, 1–2(–3) mm long, broadly enlarged basally with the enlargement perpendicular to the calyx axis, the limb cylindric or somewhat spreading, smooth or rugose, (2–)2.5–4(–6.5) mm long including the lobes, the lobes triangular, (0.5–)1–1.5 mm long, erect after anthesis, completely callose thickened and glandular, sinuses obtuse or broadly rounded and almost flat; corolla slightly narrowed at the throat, the distal portion often curving upwards, 29–32 mm long, 3–7 mm in diameter, glabrous, blue (fide *Mori & Dressler 7776*); stamens ca. 26.5 mm long, the filaments glabrous, alternately 3.5 mm and 8 mm long, the anthers including tubules alternately 25 and 20 mm long, the thecae 6–7.5 mm long; style ca. 31 mm long. *Berry* not seen.

Cavendishia melastomoides var. *coloradensis* is endemic to Cerro Colorado, Chiriquí Province. It differs from the other two varieties of *C. melastomoides* (var. *melastomoides* and var. *albiflora* both from Costa Rica) primarily in its broadly ovate to semiorbicular bracteoles which have callose-thickened, apiculate tips.

CHIRIQUÍ: Cerro Colorado copper mine development, 28 mi above San Félix, 1200–1500 m, *Croat 33211* (MO, NY). Cloud forest along continental divide on Cerro Colorado, on upper mining road 20–28 mi from San Félix, 1200–1500 m, *Croat 33351* (MO, NY). N of San Félix at Chiriquí-Bocas del Toro border, on Cerro Colorado copper mining road, *Mori & Kallunki 5987* (MO). Cerro Colorado, 50 km N of San Félix on the continental divide, 1200–1500 m, *Mori & Dressler 7776* (MO, NY).

15. **Cavendishia morii** Luteyn, Brittonia 28: 401. 1976. TYPE: Panama, *Bristan 587* (DUKE, holotype; photo NY; MO, isotype).

Epiphytic *shrub*, mature branches and twigs of the new growth terete, striate, glabrous, tan to reddish brown when dry, sometimes glaucous. *Leaves* oblong, elliptic, ovate elliptic, (7–)10–14(–16) cm long, (3–)4–6 cm wide, basally rounded, obtuse or subtruncate, apically long acuminate or abruptly short acuminate, brown or olive brown when dry, glabrous; 5(7)-plinerved, midrib and lateral nerves slightly impressed above, raised and prominent beneath, the

veinlets slightly raised but obscure on both the surfaces; petioles terete, striate, (4–)7–10(–14) mm long, 2–2.5 mm diameter, sparsely pilose when young, glabrous at maturity, dark reddish brown. *Inflorescence* 15–25-flowered; rachis bluntly angled, smooth or slightly striate, glabrous, (2.5–)7–9 cm long, 2–4 diameter at base; floral bracts smooth, glabrous, elliptic, 15–20 mm long, 8–10 mm broad, basally obtuse, apically rounded to obtuse, reddish; pedicels swollen distally, striate, glabrous, 8–10 mm long, 1 mm diameter at anthesis, later lengthening to 17 mm long; bracteoles ovate lanceolate, ca. 1.5 mm long, 0.7 mm broad, apically acute, glandular callose thickened marginally and for the distal ½. *Flowers* with the calyx glabrous, ca. 5 mm long, the tube short cylindric, coarsely ribbed, ca. 1.5 mm long, strongly enlarged basally, the limb erect and spreading to slightly campanulate, rugose, ca. 3.5 mm long including the lobes, the lobes broadly triangular to somewhat ovate apiculate, 1 mm long, erect after anthesis, completely glandular callose thickened, the sinuses obtuse; corolla slightly narrowed at the base and the throat, 18–20 mm long and ca. 4.5 mm in diameter, glabrous, the lobes triangular or oblong, obtuse, ca. 1 mm long, the tips callose thickened; stamens 18.5–19 mm long, the filaments pilose in the distal ½, alternately ca. 2 mm and 4 mm long, the anthers including tubules alternately ca. 18 mm and 16 mm long, the thecae 5.5–6.5 mm long; style ca. 19 mm long. *Berry* spherical, glabrous, ca. 11–12 mm diameter.

Cavendishia morii, endemic to Darién, is most closely related to *C. subfasciculata*. Together they share similar calyx and bracteole gland types and the unique character of callose-thickened corolla lobes. *Cavendishia morii* may be distiguished from *C. subfasciculata* by its longer, more floriferous rachises, its inflorescences fusiform in bud, its apically nonemarginate floral bracts, and smaller flowers.

DARIÉN: Cerro Pirre, *Bristan 587(3)* (DUKE, MO); *Duke & Elias 13810* (DUKE, MO). Summit of Cerro Pirre, 1000–1400 m, *Gentry & Clewell 7077* (DUKE, MO); *Gentry & Clewell 7091* (MO). Cloud forest, Cuasí-Cañá Trail between Cerro Campamiento and La Escalera, E of Tres Bocas, *Kirkbride 1306* (MO). Lower montane cloud forest, N slopes of Cerro Pirre, 700–950 m, *Mori & Kallunki 5467* (MO, NY).

16. **Cavendishia panamensis** Luteyn, Brittonia 28: 47. 1976. TYPE: Panama; Chiriquí, Boquete District, *Luteyn 3056* (DUKE, holotype; F, GH, LL, MICH, MO, NY, PMA, US, isotypes).

Erect, often arching, terrestrial *shrub*, 2.5–3 m tall; stem base ca. 2.5 cm in diameter; mature branches terete, glabrous, ca. 1 cm in diameter; bark yellowish brown; immature branches and twigs of the new growth bluntly angled or ribbed, minutely striate, glabrous. *Leaves* elliptic, lance elliptic to ovate lanceolate, 9–16 cm long, 3–6 cm wide, basally acute to narrowly obtuse, rarely rounded, apically acuminate to somewhat caudate acuminate, olive green to grayish green above and tannish green beneath when dry, glabrous but with scattered, elevated, reddish globular glands, the glands 0.1–0.2 mm in diameter along the upper leaf surface, often caducous usually leaving a reddish or blackish papillate scar; 5(–7)-plinerved, the innermost lateral nerves often arising 2–3 cm above the

base, the midrib impressed above, raised and conspicuous beneath, the lateral nerves impressed above becoming plane to slightly elevated distally with the outer lateral nerves often obscure beyond the middle, raised and conspicuous beneath, the veinlets raised and usually conspicuous above, obscure to slightly raised beneath; petioles terete, slightly flattened adaxially, rugose, (2.5–)6–8 (–10) mm long, 2–2.5(–3.5) mm in diameter, glabrous or infrequently puberluent, golden tan. *Inflorescence* viscid, 11–21(–37)-flowered, often the several lowest nodes sterile; rachis flattened, gradually tapering and often flexuous distally, conspicuously ribbed and minutely striate, glabrous or rarely puberulent, (3–) 8–17 cm long, to 5 mm in diameter at the base, pink to dark pink when fresh with minute, peltate, globular reddish glands along its length and especially at the base; floral bracts glabrous or sparsely ciliate along the distal ⅓ of the margin, oblong to oblanceolate, rarely obovate, basally narrowed to a slightly clasping base, apically rounded or narrowly obtuse to acute, (2–)3–5 cm long, (0.6–)1–2 cm wide, pink, marginally with 7–23 dark red, globular, peltate or sessile glands ca. 0.7 mm in diameter; pedicels subterete, swollen distally, striate, glabrous (11–)15–19 mm long, 1–1.5 mm in diameter, pink, with few, scattered, globular, reddish glands; bracteoles ovate to lanceolate, 1.5–2(–4) mm long, 1–2 mm wide, pink, with few, scattered, dark red, globular glands marginally and apically. *Flowers* with the calyx glabrous, 4–6 mm long, the tube cylindric or spreading, rugose to strongly ribbed, 1.5–2 mm long, 2.5 mm in diameter, not basally enlarged, green, usually with dark red, globular to disc-shaped, peltate glands obscuring the surface, the limb cylindric campanulate, smooth (2.5–)3–3.5 mm long including lobes, pale green to pinkish with scattered, globular to disc-shaped, peltate glands, the lobes triangular, obtuse, 1–1.5 mm long, 1.5 mm broad, erect after anthesis, marginally glandular callose thickened with the glands contiguous at the lobe apices, pinkish green with dark pink margins; sinuses broadly rounded; corolla constricted basally, narrowed to the throat, 2.5–3.5 cm long, 8–10 mm in diameter, glabrous, or pilose and glabrous at the constricted base, white, the lobes triangular, obtuse, 1–2 mm long; stamens 27–30 mm long, the filaments slightly coherent basally, strigose distally, alternately 4–6 mm and 10–13.5 mm long, white, the anthers including the tubules alternately 17–20.5 mm and 25–27 mm long, yellow, the thecae 7.5–11 mm long; style 25–31 mm long. *Berry* not seen.

Cavendishia panamensis like *C. chiriquiensis* is endemic to western Panama. Both species are characterized by glandular-margined floral bracts and bracteoles, and gland-covered calyx tubes. In these respects they are reminiscent of *C. pseudostenophylla*. However, the linear leaves of *C. pseudostenophylla* at once distinguish that species. *Cavendishia panamensis* differs from *C. chiriquiensis* by a basic difference in calyx lobe glands. In *C. panamensis* the callose-thickened portion of the calyx lobe is strictly marginal, while in *C. chiriquiensis* the entire calyx lobe is callose thickened and appears occasionally to break off.

CHIRIQUÍ: Boquete District, Bajo Chorro Trail, *Davidson 86* (US); *Luteyn 3056* (DUKE, F, GH, LL, MICH, MO, NY, PMA, US). Cerro Horqueta, 1800–1900 m, *Luteyn 3080* (DUKE). VERAGUAS: Cerro Tute, NW of Santa Fé, *Mendietz 562* (PMA).

17. **Cavendishia pseudostenophylla** Luteyn, Brittonia 28: 46. 1976. TYPE: Panama; Bocas del Toro, Chiriquí Trail, *Kirkbride & Duke 779* (NY, holotype, photo of type DUKE, NY; MO, isotype).

Epiphytic *liana*, mature branches terete, minutely striate, puberulent brown when dry; bark reddish brown; immature branches and twigs of the new growth subterete to bluntly angled, minutely striate, puberulent, brown. *Leaves* linear lanceolate to linear elliptic, 9–14 cm long, 1–1.5 cm wide, basally broadly obtuse or rounded, slightly cordate, apically long attenuate, acute, olive green above and reddish brown beneath when dry, glabrous, the margins strongly revolute; 3(–5)-plinerved, the midrib deeply impressed above, raised and conspicuous beneath, the lateral nerves and the veinlets raised and conspicuous above, slightly raised but obscure beneath; petioles subterete, rugose, 2–3.5 mm long, 1–2 mm in diameter, densely puberulent, dark brown. *Inflorescence* viscid, 12–20-flowered, the lowest nodes sterile; rachis long tapering, bluntly angled, minutely striate, glabrous, 5–15 cm long, ca. 1–1.5 mm in diameter, a few globular glands scattered along the rachis; floral bracts prominently veined, often somewhat ribbed, short ciliate apically, oblong or oval elliptic, basally narrowed and rounded, apically rounded or acute, (13–)19–27 mm long, (5–)7–11 mm wide, pink, the margins with sessile, globular glands to 0.2 mm in diameter, (3–)7–12 per side; pedicels subterete, to 8 mm long and 1 mm in diameter, glabrous, with a few globular glands; bracteoles oblong, oblong elliptic or oblanceolate, ca. 25 mm long, 10 mm broad at anthesis, basally rounded, apically broadly rounded, glabrous or marginally short ciliate, located ca. 1 mm below the junction of the pedicel and the calyx, completely enveloping the flowers in bud, clasping the calyx and the corolla at anthesis, with up to 15 globular marginal glands. *Flowers* with the calyx glabrous, 6.5–7.5 mm long, the tube 1.5–2 mm long, 3.5 mm in diameter, cylindric, slightly rugose, basally slightly expanded, globular glands located around margins of the basal expansion and on the tube, the limb campanulate or erect spreading, smooth or slightly ribbed, 5–6 mm long, the lobes triangular, the margins conspicuously glandular callose thickened, the thickenings nearly contiguous at the apex of the lobe, the sinuses obtuse or rounded; corolla ca. 32 mm long, 6 mm in diameter, pink, densely short pilose in the distal ⅓, the lobes triangular, ca. 2 mm long; stamens 27–28 mm long, the filaments short pilose in the distal ½, alternately 4–4.5 mm and 7.5–8 mm long, the anthers including the tubules alternately ca. 24–24.5 mm and 20 mm long, the thecae 6–7 mm long; style 31–33 mm long. *Berry* not seen.

The leaves of *C. pseudostenophylla* are about nine times longer than wide and are very reminiscent of *C. stenophylla*. Closer examination of the leaves of *C. pseudostenophylla*, however, shows them to be plinerved and apically acute, in contrast to the obscurely pinnately nerved and apically obtuse leaves of *C. stenophylla*. Other characters, especially differences in bracteole size and position also distinguish the two species. The type description was based on immature material. A more recent collection (*Mori & Kallunki 6162*) has resulted in the more detailed description above. *Cavendishia pseudostenophylla* is endemic to western Panama.

BOCAS DEL TORO: Chiriquí Trail, between Criollo and Quebrada Higueron, *Kirkbride & Duke 779* (MO, NY). VERAGUAS: Along road between Escuela Agrícola Alto Piedra and Río Dos Bocas, ca. 5–8 km from the Escuela, 730–770 m, *Croat 25938* (MO, NY). 16 km NW of Santa Fé, on road to Calovebora, 300–500 m, *Mori & Kallunki 6162* (MO, NY). NW of Santa Fé, 8.8 km from Escuela Agrícola Alto Piedra, Pacific side, *Mori & Kallunki 6168* (MO). Forest near 2nd branch of Río Santa Maria, road from Santa Fé, *Witherspoon & Dressler 8887* (MO, NY).

18. **Cavendishia pubescens** (H.B.K.) Hemsl., Biol. Centr. Amer., Bot. 2: 273. 1881.

Thibaudia pubescens H.B.K., Nov. Gen. Sp. Pl. 3: 273. 1818. TYPE: Venezuela: near Caracas, *Humboldt & Bonpland* (B, lectotype; not seen, presumably destroyed; P, isolectotype not seen, photo of isolectotype, DUKE, F, NY).
Proclesia pubescens (H.B.K.) Klotzsch, Linnaea 24: 33. 1851.
Thibaudia septemnervia Willd. ex Walp., Ann. Bot. Syst. 2: 1087. 1852, as syn., nom. illeg. Art. 34.
T. cinnamomifolia Willd. ex Walp., Ann. Bot. Syst. 2: 1087. 1852, as syn., nom. illeg. Art. 34.
Chupalon pubescens (H.B.K.) Kuntze, Rev. Gen. Pl. 2: 383. 1891.

Epiphytic and terrestrial *shrubs*, 1–3 m tall; mature branches subterete or bluntly angled, ridged, moderately short pilose, reddish brown when dry; immature branches and twigs of the new growth flattened and coarsely angled, ridged, densely short pilose with whitish or grayish trichomes ca. 0.5 mm long. *Leaves* elliptic to lanceolate, (5.5–)14–20 cm long, (1.5–)3.5–9 cm broad, basally cuneate, obtuse or rounded, apically long acuminate with a blunt tip or rarely acute, grayish green when dry, densely puberulent on both the surfaces with soft, white trichomes, persistent beneath, often glabrate above; 5(–7)-plinerved, the midrib impressed above and prominently raised beneath, the lateral nerves impressed above but plane distally, raised and prominent beneath, the veinlets plane to slightly raised but obscure on both sides; petioles subterete, rugose, coarsely ridged, (6–)9–15 mm long, 2–3.5 mm in diameter, densely short pilose. *Inflorescence* 7–11-flowered, encircled at the base by densely short-pilose bracts; rachis bluntly angled, striate, rugose, short pilose with persistent, densely white hairs, sometimes fimbriate, 1–2.5(–4.5) cm long, 2–3 mm in diameter, pink, rarely with basal cartilaginous teeth; floral bracts muricate, short pubescent both abaxially and marginally with densely white hairs, elliptic to oblanceolate, basally narrowed, apically rounded, 17–30 mm long, 7–13(–17) mm wide, pale pinkish green or whitish green, usually with small, red, clavate glands abaxially; pedicels bluntly angled, densely short pilose, often fimbriate, 6–14 mm long, 1–1.5 mm in diameter, pink but turning green; bracteoles linear to aristate, rarely oblong, 2–4.5 mm long, to 1 mm wide, densely pubescent and glandular fimbriate. *Flowers* with the calyx pubescent with densely matted white or tan trichomes, glandular fimbriate, 5.5–6.5(–9) mm long, the tube cylindric, 2.5–4 mm long, not basally enlarged, green, the limb campanulate or spreading, (2.5–)3.5 mm long, whitish to pinkish green, the lobes oblong, broadly triangular, obtuse or broadly rounded and apiculate, 1.5–2(–3) mm long, connivent after anthesis, pinkish green, the sinuses obtuse; corolla cylindric or bottle-shaped, slightly constricted basally, narrowed to the throat, (14–)17–19 (–22) mm long, 8 mm in diameter, white or in age tinted with pink, densely short pilose with white or tawny trichomes, the lobes triangular, wide spreading

at anthesis; stamens 11–15.5 mm long, the filaments alternately 2.5–4 mm and 3.5–6 mm long, white, the anthers including the tubules alternately 8–11 mm and 9.5–13 mm long, brownish orange, the thecae 2.5–4 mm long; style glabrous or rarely distally pilose, 13.5–17 mm long. *Berry* densely puberulent, 8–14 mm in diameter.

Cavendishia pubescens is widespread in the Andes of South America from Bolivia to Venezuela. Its most northwestern location is Volcán Chiriquí, Panama, where it is common on the western side of Volcán Chiriquí along the steep roadside slopes northwest of El Hato. It is readily distinguished by pale pinkish to whitish green floral bracts, densely short pilose white corollas, densely pilose to almost wooly calyces, and by persistently puberulent leaves and fruits. The densely matted hairs of the calyx are in themselves enough to distinguish the taxon.

Cavendishia pubescens is closely related to *C. crassifolia*. Several collections from the area between El Hato and Cerro Punta in the vicinity of Volcán Chiriquí suggest the possibility of hybridization between the two species. Such collections are noted below with an asterisk.

CHIRIQUÍ: Road to Cerro Pando, 6 km NE of El Hato, 1840 m, *Correa 1384* (DUKE). Road to Bambito, beyond the llanos, 1840 m, *Correa & Lazor 1414* (DUKE, MO). Boquete, *Davidson 649* (A, F, MO, US). 1.5 mi S of Cerro Punta, 1850 m, *Graham 288* (GH, MICH). Road NW of El Hato towards Costa Rica, 1690 m, *Luteyn 853* (DUKE, MO). Pasa Ancho, 1840 m, *Luteyn 3053** (DUKE), *3054* (DUKE, F, MO, NY). Road NW of El Hato towards Costa Rica, 1690 m, *Luteyn 3055* (CAS, DUKE, F, GH, LL, MICH, MO, MSU, NY, UC, US, WIS). Road 2 km above Bambito towards Cerro Punta, *Luteyn & Wilbur 4652** (DUKE, F, GH, MICH, MO, NY, US). Boquete, *Seemann 1613* (BM, K). Just S of Boquete, *Stern et al. 1959* (MICH, MO, US). At opening to canyon to Bambito, 1540 m, *Tyson 5862** (FSU, MO). NE of Cerro Pando, 1500 m, *Wilbur et al. 11015* (CAS, DUKE, F, FSU, G, GH, LL, MICH, MO, MSU, NY, PMA, UC, US, WIS). Slopes between Nueva Suiza and Bambito, 1690 m, *Wilbur et al. 11878, 11879** (both DUKE).

19. **Cavendishia quercina** A. C. Smith, Contr. U.S. Natl. Herb. 28: 450. 1932. TYPE: Costa Rica; San José, Cerro Carizia, *Pittier 14030* (US, holotype; photo of holotype, DUKE, NY; NY, isotype).

Terrestrial and epiphytic *shrubs*, 0.5–2 m tall; stem base to 8 cm in diameter; mature branches terete or subterete, minutely striate, densely puberulent, becoming glabrate, green or often with a tinge of maroon but drying reddish brown; bark grayish or dark brown but drying grayish; immature branches and twigs of the new growth subterete or bluntly angled, sometimes conspicuously striate, usually densely short pilose with grayish or whitish trichomes. *Leaves* oblong, oblong ovate or ovate, 2.5–7.5 cm long, (1–)1.5–3.5 cm wide, basally rounded and subcordate, the sinus often as long as the petiole, leaves hence appearing sessile and somewhat clasping, apically rounded, obtuse, or often subacute in the young leaves or the leaves produced at end of the season, green to metallic blue green when dry, usually densely short pilose on both the surfaces along the leaf margins, the midrib, and the lateral nerves when young, the pubescence usually persistent only on the upper surface; 3–5(–7)-plinerved with the lateral nerves often arising well above the base thus the leaves sometimes appearing pinnate distally; midrib and lateral nerves slightly impressed

above, conspicuously raised beneath, the lateral nerves sometimes slightly raised above, the veinlets impressed, plane or raised above and usually slightly raised but inconspicuous beneath; petioles subterete and often flattened adaxially, often coarsely rugose, (1–)2–4(–6) mm long, 1.5–2 mm in diameter, dark reddish brown when dry, densely short, white puberulent, often becoming glabrate. *Inflorescence* 12–20(–53)-flowered; rachis obtusely angled, frequently muricate, glabrous or densely hirsute, 2–12 cm long, 2–3 mm in diameter at the base, dark pink but turning greenish at anthesis; floral bracts glabrous or marginally short ciliate, smooth or rarely ribbed when dry, commonly marginally glandular fimbriate, the fimbriae often caducous, oblong or oblong elliptic, basally rounded and often somewhat clasping, apically obtuse or rounded, (9.5–)11–18 (–23) mm long, 6–10(–13) mm broad, red; pedicels subterete, often angled, striate and rugose, swollen at both ends, sparsely to densely hirsute or rarely glabrate, (6.5–)10–14(–18) mm long, 0.5–2 mm in diameter, dark pink but turning greenish at anthesis; bracteoles oblong or oblong ovate, 1–3(–5.5) mm long, 0.5–1(–2.5) mm wide, densely marginally glandular fimbriate, glabrous or ciliate or apically short pilose. *Flowers* with the calyx sparsely to densely hirsute, rarely glabrous, (5.5–)6–8(–9) mm long, the tube short cylindric, often 5-ribbed, rugose, 1.5–2.5(–3) mm long, basally enlarged, the enlargement conspicuous and diverging almost at right angles, marginally undulate or only slightly lobed, dark purplish pink but turning greenish at anthesis, the limb cylindric, erect spreading or rarely campanulate, smooth to rugose or sometimes ribbed, (3.5–)4–6(–6.5) mm long including the lobes, red basally and green above but totally red at anthesis, the lobes narrowly or sometimes broadly triangular, 1–2.5 mm long, 1.5–3 mm wide, erect after anthesis, marginally short ciliate and provided along each side of the lobe with 3–5 stout, callose thickened, glandular fimbriae, these rarely fusing into one oblong, concave gland to 0.5 mm long, sinuses broadly rounded and ciliate; corolla slightly constricted and glabrous basally, densely pilose distally, rarely glabrous, (8.5–) 11.5–15(–17.5) mm long and 2.5–4.5 mm in diameter, the tube pale pinkish basally, pale green above, the limb and the lobes whitish to pinkish green, the lobes oblong, obtuse, to 2 mm long, erect or slightly spreading at anthesis; stamens 8–15 mm long, the filaments pilose distally, alternately either 2–5 mm or 3–8 mm long, pink basally, white above, the anthers including tubules alternately 5–9.5 mm and 6.5–12 mm long, orange, the thecae 1–4 mm long; style 9–16 mm long. *Berry* 9–10 mm in diameter.

Cavendishia quercina has only been collected once in western Panama. It is scattered and infrequent in Costa Rica. The single collection from Volcán Chiriquí shows no significant variation from the more common Costa Rican material.

CHIRIQUÍ: Valley of upper Río Chiriquí Viejo, *White & White* 89 (MO).

20. **Cavendishia revoluta** Luteyn, Brittonia 28: 44. 1976. TYPE: Panama; *Foster & Kennedy 1906* (DUKE, holotype; photo NY).

Terrestrial *shrub*, glabrous throughout; mature branches terete, striate, minutely rugose, brown to reddish brown when dry; immature branches subterete,

bluntly angled, striate, minutely rugose, light brown when dry. *Leaves* thickly coriaceous, lanceolate to lance ovate, 11–16 cm long, 5–9 cm wide, basally short attenuate, somewhat decurrent, apically acute, somewhat cuspidate, the margins entire and tightly revolute, olive to light greenish brown when dry; 5–7-plinerved, the midrib and the lateral nerves weakly impressed above, sometimes slightly elevated distally, the veinlets raised and conspicuous above, the nerves raised and conspicuous beneath, or with the veinlets sometimes obscure; petioles subterete, sometimes flattened adaxially, rugose 4–10 mm long, 3–5.8 mm in diameter, light olive brown to reddish brown. *Inflorescence* 9–15-flowered; rachis stout, bluntly and coarsely angled, white speckled, ribbed, rugose, 3–4 cm long, 4–5 mm in diameter at the base, cream pink; floral bracts smooth, marginally glandular fimbriate, elliptic, concave, 14–20 mm long, 11–12 mm broad, basally cuneate and truncate, apically rounded; pedicels becoming wider distally, striate, 3.5–7.5 mm long, 1.5–2.5 mm in diameter; bracteoles oblong, marginally glandular fimbriate, 2–3 mm long, about 2 mm broad. *Flowers* with the calyx 9–11 mm long, the tube with short, stout, reddish, glandular fimbriae when immature, cylindric to barrel-shaped, 4–5 mm long, 4.5–5.5 mm in diameter not basally enlarged, the limb cylindric, smooth, 5–6.6 mm long including the lobes, the lobes oblong to broadly triangular, marginally densely glandular fimbriate when young, soon caducous, mature margins dark red, appearing thinner than the main body of the limb, 2–2.5 mm long, 2.5–3 mm broad, the sinuses acute; corolla immature; style persistent, 10–11 mm long. Mature *berry* not seen.

Cavendishia revoluta is endemic to Cerro Jefe, Panama Province. Its most outstanding feature is the overall coarse appearance, exemplified by the thick, hard leaves with tightly revolute margins. According to *Foster & Kennedy 1906*, the leaves have the "distinct smell of wintergreen." To our knowledge this odor is otherwise found only in *C. quereme* (H.B.K.) Benth. & Hook. from Costa Rica and Colombia.

PANAMÁ: Near top of Cerro Jefe, 900 m, *Foster & Kennedy 1906* (DUKE); *Gentry 5524* (MO, NY). Top of Cerro Jefe, 830–925 m, *Tyson et al. 4391* (FSU, MO).

21. **Cavendishia santafeënsis** Luteyn, Brittonia 28: 48. 1976. TYPE: Panama; Veraguas, 5 mi W of Santa Fé, *Croat 22986* (MO, holotype; photo of type, DUKE, NY).

Epiphytic *shrub*, glabrous throughout; mature branches and twigs of the new growth subterete, smooth or striate, reddish brown when dry. *Leaves* elliptic, lance elliptic or oblong lanceolate, (8–)10–19 cm long, (2.5–)4.5–6.5 cm wide, basally rounded or narrowly obtuse, apically short acuminate; 3–5-plinerved, the midrib and the lateral nerves impressed above, raised and conspicuous beneath, the outer pair of the lateral nerves anastomosing with the secondary nerves midway up the leaf, the veinlets slightly raised on both the surfaces but conspicuous only above; petioles terete, rugose, ridged, 7–10 mm long, 2–3 mm in diameter, dark brown when dry. *Inflorescence* 9–12-flowered, the lowest few nodes sterile; rachis subterete, stout, 1.5–2.5 cm long, ca. 5 mm in diameter at base; floral bracts thin and translucent when dry, spatulate, apically

rounded and deeply emarginate, 33–45 mm long, 15–20 mm wide at the top, narrowing sharply to 2–6 mm at the base, pale reddish violet, lamina with tiny, red, clavate abaxial glands; pedicels striate, 8–13 mm long, 1–1.5 mm in diameter; bracteoles similar to the floral bracts but 36–44 mm long, 10–12 mm wide at the top, narrowing to ca. 1 mm at the base, conspicuously imbricate distally in bud, the margins without glandular fimbriae or callose thickenings. *Flowers* with the calyx 8–8.5 mm long, the tube cylindric, bluntly 5-angled, 3–3.5 mm long, shallowly enlarged basally, the enlargement undulate but not lobed, the limb cylindric, 5 mm long including the lobes, the lobes narrowly triangular, acute, 3–3.5 mm long, erect after anthesis, marginally glandular callose thickened with oblong glands extending marginally along each side of the lobe, sinuses obtuse; corolla glabrous ca. 42.5 mm long, 7 mm in diameter, white, the lobes 3 mm long, purple; stamens 37–38 mm long, the filaments alternately ca. 2.5 mm and 10.5 mm long, the long filaments puberulent, the anthers including the tubules alternately ca. 36 mm and 28.5 mm long, the thecae 14–15 mm long. *Berry* not seen.

Cavendishia santafeënsis has been collected only three times and much more material is needed before an adequate summation of its characters can be made. It is distinctive, however, in its large bracteoles which reach 35–45 mm in length. These are seemingly the largest of any known *Cavendishia*. The marginally callose-thickened calyx lobes are also distinctive. The species is endemic to the area north of Santa Fé de Veraguas.

VERAGUAS: 5 mi W of Santa Fé on road past the Escuela Agrícola Alto Piedra, Pacific side of divide, 800–1200 m, *Croat 22986* (MO). Along road past the Escuela Agrícola Alto Piedra, ca. 1000 m, *Luteyn & Wilbur 4570* (DUKE). 6–7 km W of Santa Fé, road past agricultural school, 1000 m, *Nee 9724* (DUKE, MO, NY).

22. **Cavendishia stenophylla** A. C. Smith, Ann. Missouri Bot. Gard. 27: 327. 1940. TYPE: Panama; *Allen 1880* (NY, holotype; photo of holotype, DUKE; MO, isotype).—FIG. 5.

Epiphytic and terrestrial *shrubs* ca. 1.5 m tall; stem base to 2 cm in diameter; mature branches terete or obtusely angled, smooth or minutely striate, glabrate, green or brown when fresh but drying tan or reddish brown; immature branches and new twigs terete, obtusely angled or conspicuously flattened, minutely striate, glabrate or densely short pilose. *Leaves* linear, linear lanceolate or elliptic lanceolate, averaging 5–6 times longer than wide, (4.5–)7.5–12(–14.5) cm long, (0.5–)1–2(–2.5) cm wide, basally narrowing, rounded and usually slightly cordate, apically long attenuate to an ultimately blunt tip, reddish to olive brown when dry, glabrous, marginally usually strongly revolute, rarely flat; pinnately nerved, the lowest primary nerves sometimes arcuate to about the middle then anastomosing with the remaining veins forming a collective nerve which extends to the apex, the midrib deeply impressed above and conspicuously raised beneath, the lateral nerves and the veinlets raised and conspicuous above, slightly raised but obscure beneath; petioles subterete, rugose and often longitudinally ribbed, 3.5–6.5(–9) mm long and 1–2.5 mm in diameter, densely short pilose adaxially, becoming glabrate. *Inflorescence* solitary or rarely two in terminal axils,

FIGURE 5. *Cavendishia stenophylla* A. C. Smith.—A. Habit (×3/5).—B. Stamens, ventral and lateral views (×1 3/5). [After *Luteyn 3102* (DUKE).]

8–28-flowered, the lowest 3–8 nodes usually sterile, viscid; rachis conspicuously bluntly angled, minutely striate, glabrous, purple, 5.5–13 cm long, 1–2.5 mm in diameter; floral bracts conspicuously nerved, glabrous, concave or hood-shaped, ovate, 3–6.5 mm long, 2.5–4.5 mm wide, basally rounded and truncate, somewhat auriculate, apically acute or obtuse, the distal ⅔ of the margin callose thickened, dark purple with greenish tinge; pedicels subterete, striate, apically swollen, glabrous, 11–18(–24) mm long, 0.5–1(–1.5) mm in diameter, dark purple; bracteoles positioned one-third to halfway up the pedicel, conspicuously nerved, glabrous, concave, ovate, 1.5–2.5(–3) mm long, (0.5–)1.5(–3) mm wide, basally continuous (not articulated) with the tissue of the pedicel, apically acute, the distal ⅔ to ½ glandularly callose thickened, dark purplish green. *Flowers* with the calyx glabrous, (5–)6–7(–8) mm long, sometimes slightly stipitate, the tube cylindric, rugose and ribbed, the surface often muricate, (1.5–)2–3(–4.5) mm long, basally strongly enlarged and deeply lobed, green when immature, dark purple at anthesis but turning greenish after anthesis, the limb cylindric or spreading, rarely campanulate, ribbed, (2–)4–4.5(–5.5) mm long including the lobes, the lobes triangular, 1–1.5(–2) mm long, (1.5–)2–2.5 (–3) mm wide, erect after anthesis, completely callose thickened or the margins rarely slightly thinner than the main body, purple, the sinuses obtuse to broadly rounded; corolla slightly constricted basally, narrowed at the throat, outside densely short pubescent, the trichomes usually white, 0.2–0.4 mm long, rarely glabrous, sparsely pilose within, (16–)18–21.5(–22) mm long, 4–8 mm in diameter, pale purple at the constricted base, purple above, the lobes triangular, 1–1.5 mm long, glabrous, reflexed at anthesis often exposing the tips of the anthers; stamens 15.5–19.5 mm long, the filaments alternately 2–3.5 mm and 5–7.5 mm long, white, with medially pilose long filaments and distally pilose short filaments, sometimes glabrous, the anthers including the tubules alternately 12.5–14.5 mm and 15.5–18 mm long, orange, the thecae alternately 4–5.5 mm and 5.5–6.5 mm long; style sigmoid, exserted at anthesis, green. *Berry* glabrous, 12–15 mm in diameter.

Cavendishia stenophylla is endemic to central Panama where it occurs from 700–1,000 m elevation. It is distinguished by the combination of linear leaves with strongly revolute margins, and callose-thickened floral bracts. Linear leaves are found in only one other Central American species, *C. pseudostenophylla*. The basic venation difference between these two species has been mentioned in the discussion of *C. pseudostenophylla*. Callose-thickened floral bracts are unique to *C. stenophylla*.

COCLÉ: Hills N of El Valle, 1000 m, *Allen 2162* (A). La Mesa, *Allen 2373* (A, MO). Hills N of El Valle, *Allen 3551* (MO, US). Slopes of Cerro Pilón near El Valle, 700–900 m, *Duke 12049(3)* (MO). Between Cerro Pilón and El Valle, 700–900 m, *Duke & Dwyer 13986(1)* (MO). El Valle, WEPCOR site, *Kirkbride 1086* (MO). La Mesa, 850–870 m, *Luteyn 3102* (DUKE). Trail to Los Llano, 800–850 m, *Luteyn 3153* (DUKE, NY). Trail to Las Minas, 800–900 m, *Luteyn 3161* (DUKE, F, MO), *4063* (DUKE, F, MO, US). La Mesa, *Luteyn 4089* (DUKE, F, MO, NY); *Weaver & Foster 1635* (DUKE). PANAMÁ: Hills above Campana, 600–800 m, *Allen 1880* (MO, NY). Cerro Campana forest, 700–900 m, *Allen 2422* (A); *Blum et al. 2372* (FSU, MO); *Lewis et al. 1921* (MO, UC); *Luteyn & Kennedy 1819* (DUKE); *Luteyn 3083* (DUKE); *Luteyn 3191* (DUKE, F, NY); *Luteyn 3992*

(DUKE, F); *McDaniel 6841* (FSU, MO); *Mori & Bolten 7676* (MO, NY). Cerro Campana, summit and upper trail, *Witherspoon & Witherspoon 8477* (MO, NY).

23. **Cavendishia subfasciculata** Luteyn, Brittonia 28: 50. 1976. TYPE: Panama; Chiriquí, Boquete District, *Luteyn 3743* (DUKE, holotype; F, GH, LL, MO, NY, PMA, US, isotypes).

Epiphytic *shrub* 7–10 dm tall or terrestrial and 1–3 m tall; stem base to 2.5 cm in diameter; mature branches terete, smooth or minutely striate, glabrous, green but drying tan to reddish brown, usually with a thin, whitish waxy layer over the branches; bark reddish brown; immature branches and twigs of the new growth subterete to bluntly angled, striate, often coarsely ridged, glabrous, reddish brown when dry. *Leaves* lanceolate to lance elliptic, (3–)5–9(–11) cm long, (1–)2–4 cm wide, basally obtuse or rounded, lamina often short decurrent along the petiole, apically short acuminate, often abruptly so, grayish to brownish green when dry, glabrous or often with numerous short trichomes at the base of the midrib adaxially, usually soon glabrate; 5(–7)-plinerved, the midrib plane or more commonly weakly impressed above, the lateral nerves usually raised and conspicuous, rarely weakly impressed above, the veinlets all raised and conspicuous to obscure above, the nerves raised beneath but the veinlets obscure; petioles subterete, usually flattened adaxially, rugose and often coarsely ridged, 7–13 mm long, 1.5–2 mm in diameter, glabrous to weakly pilose adaxially when young, often glabrate when mature. *Inflorescence* (2–)3–6(–9)-flowered, obconic to spherical in bud; rachis flattened, bluntly angled, striate, viscid, glabrous, (0.3–)0.6–1.2(–3.2) cm long, pale green, usually with minute cartilaginous teeth at the base; floral bracts usually translucent when dry, glabrous, smooth or rarely slightly ribbed, usually with minute, red, glandular fimbriae abaxially, oblong to oblanceolate or oblong lanceolate, basally narrowed and somewhat auriculate, apically rounded or obtuse, usually emarginate, or when young with the notch almost completely filled with callose tissue, (1.5–)2–3(–4) cm long, 0.5–1(–2) cm wide, pale green, but suffused with pink along the margins and at the base, drying green; pedicels swollen distally, ridged, glabrous (6–)8–13(–15) mm long and (0.5–)1–1.5 mm in diameter, pale green to cream colored and often suffused with pink, occasionally with cartilaginous teeth at the distal end; bracteoles linear lanceolate, 1–2.5(–3) mm long, 0.5–1 mm wide, apically acuminate and glandular callose thickened on the distal ½–⅔, pale green. *Flowers* with the calyx glabrous, 5–7(–10) mm long, pale green but sometimes suffused with pink, the tube cylindric, weakly rugose, strongly ribbed, (1.5–)2–3(–4) mm long, basally enlarged, deeply lobed, the lobes straight, extending to or just below the pedicel articulation, the limb campanulate to cylindric, smooth or weakly ribbed and minutely papillate when dry, (2.5–)3.5–4.5(–6) mm long including the lobes, the lobes triangular, (0.7–)1–1.5(–2) mm long, 2–3 mm wide, sometimes flaring outward at anthesis, later erect, glandular callose thickened throughout or only for the distal ⅔, the sinuses obtuse, broadly rounded or flat; corolla slightly constricted basally, narrowed to the throat, often translucent when dry, 20–24(–30) mm long, 5–7 mm in diameter, glabrous or rarely pilose, whitish at the base and the apex, otherwise pinkish violet to rose red, the

lobes triangular or oblong, acute, ca. 1 mm long, reflexed at anthesis, the tips often callose thickened, white with pinkish or violet margins; stamens 19–24.5 mm long, the filaments densely pilose, alternately 2.5–5 mm and 5–10 mm long, pale green, the anthers including tubules alternately 13–20 mm and 17–22 mm long, tawny, the thecae 4.5–7 mm long; style 22–29 mm long, green. *Berry* ca. 9 mm in diameter.

Cavendishia subfasciculata, endemic to western Panama, may be distinguished from *C. megabracteata* by its overall smaller size, by its habit which presents a fuller and more dense appearance, by the green floral bracts as compared with the pinkish or pale purple bracts of *C. megabracteata*, by slightly decurrent leaf bases, and by the leaf venation.

CHIRIQUÍ: Cerro Punta, 2000 m, *Allen 1535* (MO). Cerro Copete, 2460–2610 m, *Allen 4860* (G, MO, NY, US). Las Cumbres near Cerro Punta, *Croat 13701* (DUKE, MO, NY), *26305* (MO); *Croat & Porter 16082* (MO). Cerro Horqueta, 2000 m, *Hagen & Hagen 2029* (GH, NY). Bajo Mono, 1500–2000 m, *Luteyn 3717* (DUKE, F, GH, MO, NY). Boquete District, E side of Cerro Horqueta, 1700–1800 m, *Luteyn 3743* (DUKE, F, GH, LL, MO, NY, PMA, US); *Luteyn & Wilbur 4588* (DUKE, NY). Cerro de Lino above Boquete, 1300–1560, *Pittier 3036* (F, US). VERAGUAS: NW of Santa Fé, below summit of Cerro Tute, *Mori & Kallunki 5274* (MO, NY).

EXCLUDED SPECIES:

Cavendishia splachnoides A. C. Smith (Contr. U.S. Natl. Herb. 28: 471. 1932) is known only from the type locality in southern Darién Province (Cerro de Garagará, Sambú Basin, 500–974 m). The holotype (*Pittier 5647*, US) and an additional collection (*Pittier 5659*, US) are in such poor condition, however, that it is not possible to include them in this treatment. This species belongs to a complex of lowland taxa extending into Colombia much in need of additional collecting and study.

Cavendishia bomareoides A. C. Smith from Cerro de Garagará, Darién Province was misidentified and must be excluded from the flora of Panama. The Panamanian collection (*Pittier 5651*, US) attributed to this species represents a sterile twig of *C. fusiformis*.

Cavendishia miconioides A. C. Smith is a South American species (Luteyn, 1976) and those specimens from Chiriquí Province which have been identified as *C. miconioides* are a small-leaved form of *C. crassifolia*.

6. DIDONICA

Didonica Luteyn & Wilbur, Brittonia 29: 255. 1977. TYPE: *D. pendula* Luteyn & Wilbur.

Epiphytic *shrub*. *Leaves* alternate, estipulate, coriaceous, entire, plinerved. *Inflorescence* of solitary, axillary, pendulous flowers; pedicels 4–6 times as long as the flower and continuous with it; bracts and bracteoles glandular fimbriate. *Flowers* with the hypanthium glabrous, terete; calyx lobes 5, erect; corolla campanulate cylindric, 5–6-parted; stamens 10–12, the filaments distinct, ciliate, narrowing to a connective which extends to the base of the tubules, the anthers finely granular, the tubules slightly shorter than the thecae, somewhat

spreading, dehiscing by oval, latrorse clefts; style glabrous, the stigma peltate, the ovary inferior. *Fruit* unknown.

Didonica is a monotypic, Panamanian endemic characterized by solitary, pendent flowers on an elongate pedicel continuous with the calyx and by anthers dehiscing by oval, latrorse clefts which do not extend to the apex of the tubule.

1. **Didonica pendula** Luteyn & Wilbur, Brittonia 29: 255. 1977. TYPE: Panama, *Dressler 5170* (DUKE, holotype; photo of holotype, NY).—FIG. 6.

Epiphytic *shrub* 7–10 dm tall; mature stems subterete, smooth or minutely striate, glabrous or puberulent, dark blackish red when dry; immature stems and twigs of the new growth subterete, striate, glabrous or puberulent, brownish or graying when dry; pseudostipules ca. 2 mm long. *Leaves* lance elliptic to ovate, (4.5)6–9 cm long, (1.5)2–5 cm wide, glabrous, basally rounded to obtuse or shortly cuneate, apically short to long acuminate, entire, green to olive green when dry, glandular fimbriate beneath but fimbriae soon deciduous; 5(–7)-plinerved, the midrib impressed above, thickened and raised for the proximal 1–1.5 cm, elevated beneath, the lateral nerves and the veinlets slightly raised on both the surfaces; petioles subterete, rugose, glabrous, slightly winged laterally, 5–10 mm long, 1.5–2 mm in diameter, dark reddish brown when dry. *Inflorescence* with the rachis 1.5 mm long; pedicels terete, minutely ribbed, glabrous, 15–18 cm long, 0.3–0.5 mm in diameter; floral bract ovate, ca. 1 mm long, marginally glandular fimbriate; bracteoles nearly basal, aristate, ca. 1.5 mm long, marginally glandular fimbriate; hypanthium and calyx glabrous, 10–12 mm long, the tube obconic, muricate, 3.5–5 mm long. *Flowers* with the calyx limb campanulate, conspicuously nerved, 6.5–7 mm long including the lobes, the lobes broadly ovate, apiculate, 2.5 mm long, 5 mm wide at base with acute sinuses; corolla campanulate cylindric, glabrous, ca. 22 mm long, pink, thin and membranous when dry, the lobes broadly ovate, 2.5 mm long, 6 mm wide; stamens ca. 12 mm long, all alike, the filaments ciliate, ca. 4.5 mm long, 2 mm wide at base, narrowing to the connective, the connective extending to the base of the tubules, the anther including the tubules ca. 10 mm long, the thecae 6.8–7.5 mm long, minutely granular, the tubules slightly spreading, 3.0–3.2 mm long, pilose adaxially, dehiscing by oval, latrose clefts 1.5–2 mm long, but the clefts not extending to the apex of the tubule; style glabrous, 16–18 mm long, the stigma peltate. *Fruit* unknown.

In spite of marked morphological variation we have included both of the known collections under the same binomial. The specimen from Coclé (*Allen 3760*) has glabrous twigs, ovate, short-acuminate leaves about 3–5 cm wide and pentamerous flowers. Dressler's specimen from Veraguas (*5170*) has puberulent twigs, narrowly lanceolate, long acuminate leaves about 2 cm wide and flowers with 5-lobed calyces, 6-lobed corollas and 12 stamens. Additional collections are needed to evaluate these differences and to complete our understanding of the morphology of the species.

COCLÉ: El Valle de Antón, crest of Cerro Pajita, 1100 m, *Allen 3760* (MO). VERAGUAS: Third branch of Río Santa María, 10–14 km NW of Santa Fé, 650–750 m, *Dressler 5170* (DUKE).

FIGURE 6. *Didonica pendula* Luteyn & Wilbur. Habit (×½). [After *Dressler 5170* (DUKE).]

7. DISTERIGMA

Disterigma (Klotzsch) Niedenzu, Bot. Jahrb. Syst. 11: 160, 209. 1889. LECTOTYPE: *D. empetrifolium* (H.B.K.) Drude.

Vaccinium sect. *Disterigma* Klotzsch, Linnaea 24: 57. 1851.
Vacciniopsis Rusby, Bull. Torrey Bot. Club 20: 433. 1893. TYPE: *V. ovata* Rusby = *Disterigma ovatum* (Rusby) Blake.

Bushy to straggly, terrestrial or epiphytic *shrubs*. *Leaves* alternate, less than 3 cm long, short petiolate, coriaceous, usually obscurely nerved. *Inflorescence* an axillary cluster of 1–6, often subsessile flowers subtended by a few, minute,

subcoriaceous bracts and borne on basally bracteate and always apically bibracteolate pedicels. *Flowers* obscurely articulate with the pedicel and embraced by the closely subtending bracteoles; hypanthium campanulate to short cylindric; calyx lobes 4–5, suberect; corolla subcylindric or campanulate cylindric, 4–5-lobed; stamens usually twice as many as the corolla lobes but rarely of the same number as the lobes, the filaments ligulate, the anthers dorsally attached near the base, membranous, prolonged into (1)2 tubules and dehiscing by elongate, elliptical, introrse clefts; style filliform and about as long as the corolla, the stigma truncate; ovary inferior, (3)4–5-celled with numerous ovules and surmounted by a fleshy, mound-like ring. *Berry* coriaceous.

Disterigma is a small genus of about 25 species ranging from the highlands of Guatemala south to Bolivia and east into the Guianas.

Literature:

Smith, A. C. 1933. The genera *Sphyrospermum* and *Disterigma*. Brittonia 1: 203–232.

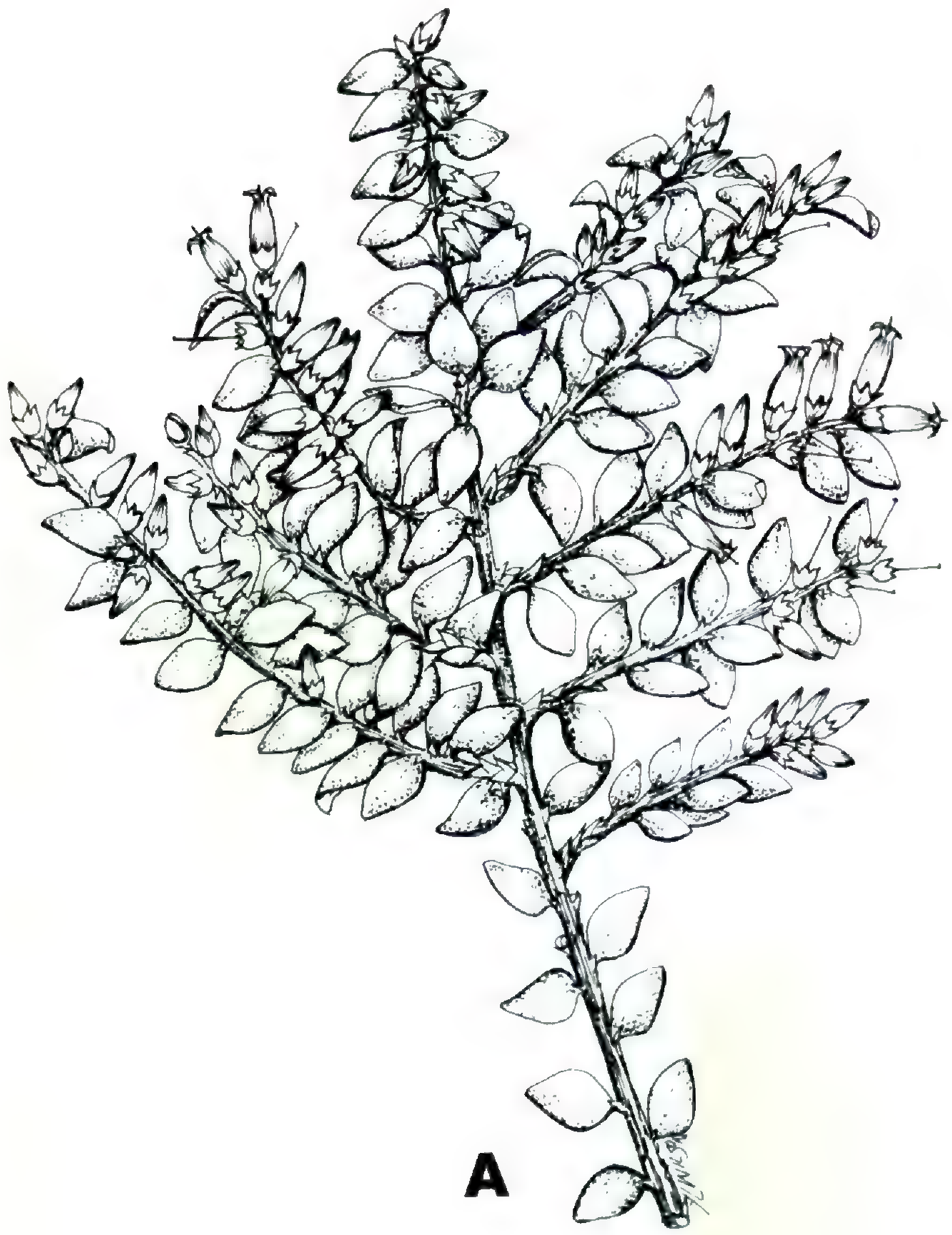
Wilbur, R. L. 1974. The Central American species of the genus *Disterigma* (Ericaceae: Vaccinieae). Bull. Torrey Bot. Club 101:245–249.

a. Lobes of calyx and corolla 3; corolla deep red; stamens 6 ..... 4. *D. trimerum*
aa. Lobes of calyx and corolla 4; corolla white or pale greenish white; stamens 8.
  b. Thecae of anthers both emptying into a single tubule about 1.5 mm long; leaves mostly more than 1 cm long and wide and with an apiculus 1–2 mm long ..... 5. *D. utleyorum*
  bb. Thecae of anthers each emptying into its own tubule (i.e. tubules 2 per anther) 2 mm long or longer; leaves mostly 1 cm or less long and wide and nonapiculate.
    c. Leaf-blades 2.5 times as long as wide or less and 4 mm wide or wider; calyx lobes eciliate; calyx tube 4-angled in cross-section; corolla tube 6–8 mm long ..... 1. *D. humboldtii*
    cc. Leaf-blades 3 or more times as long as wide and 2.5–4.5 mm wide; calyx lobes ciliate; calyx tube terete or nearly so in cross-section; corolla tube 4–6 mm long.
      d. Calyx lobes 2–2.5 mm long; leaves typically widest at or near the middle, usually linear, mostly about 4 times as long as wide; Prov. de Darién ..... 3. *D. panamense*
      dd. Calyx lobes less than 2 mm long; leaves typically widest above the middle, oblanceolate, mostly about 3 times as long as wide; Prov. de Panamá ..... 2. *D. luteynii*

1. **Disterigma humboldtii** (Klotzsch) Niedenzu, Bot. Jahrb. Syst. 11: 224. 1889.—FIG. 7.

Vaccinium humboldtii Klotzsch, Linnaea 24: 57. 1851. TYPE: S. America, *Humboldt 2065* (B, holotype, not seen and presumably destroyed).
V. pachyphyllum Hemsl., Biol. Centr. Amer. Bot., 2: 275. 1881. TYPE: Costa Rica, *Endres 154* (K, holotype, not seen; photo of holotype, NY).
Disterigma pachyphyllum (Hemsl.) Blake, J. Wash. Acad. Sci. 16: 365. 1926.
D. mayanum Lundell, Wrightia 5: 85. 1975. TYPE: Guatemala; Dept. Baja Verapaz, *Lundell & Contreras 18936* (LL, not seen).

Bushily compact to straggly, terrestrial or epiphytic *shrubs* (2–)5–10(–12) dm tall; branchlets ridged and grooved and indistinctly 3-angled to irregularly 4-angled, typically setose with tawny to chocolate brown trichomes mostly



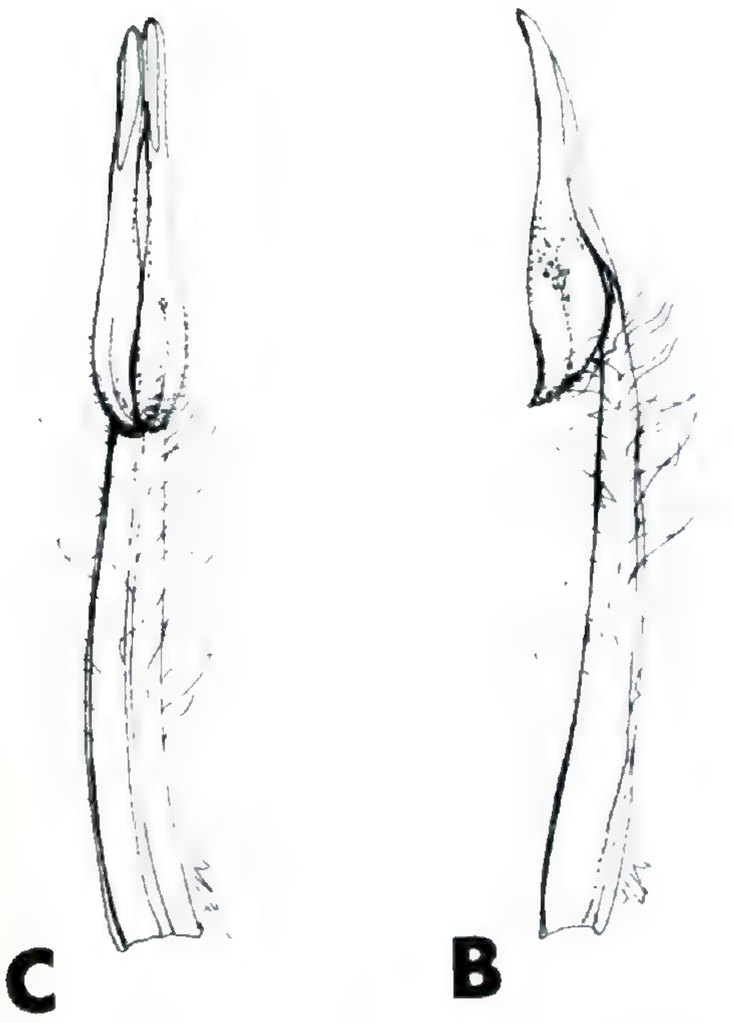


FIGURE 7. *Disterigma humboldtii* (Klotzsch) Niedenzu.—A. Habit (×⅗).—B–C. Stamens.—B. Lateral view (×6).—C. Ventral view (×6). [After *Wilbur & Luteyn 18803* (DUKE), Costa Rica.]

0.5 to 1.2 mm long or moderately to densely puberulous, becoming glabrate and terete; internodes short on lateral branchlets, usually less than half as long as the nearest leaf, often only 1–2 mm long, but 1–2 times as long as the nearest leaves on fast growing leading shoots. *Leaves* coriaceous, entire, ovate to elliptic to almost orbicular, 6–10(–16) mm long, 4–6(–9) mm wide, apically obtuse to rounded, basally rounded, glabrate or with a sparse scattering of appressed, clavate trichomes 0.2 mm long or less on the lower surface, commonly with a dense but short, apical tuft or marginal cilia, the midvein slightly impressed above, the venation otherwise completely obscure both above and beneath, dark green above and pale green beneath, this distinction persisting when dried; petioles 1(–2) mm long, sparingly to moderately spreading short pubescent. *Inflorescence* of solitary flowers to 2–3 per axil; pedicels ca. 0.5–1(–1.5) mm long; bracts 2–3, basal, broadly clasping, 2–3 times broader than long; bracteoles glabrous, 2, broadly clasping, oblong, truncate, 3–4 mm long and nearly as broad, borne just below and embracing the base of the flower. *Flowers* with the hypanthium 4-angled, campanulate, glabrous, ca. 1 mm long, 1–1.5 mm in diameter; calyx lobes 4, erect to slightly spreading, lance deltoid, acute, 1.5–2.5 mm long, entire and eciliate, 1.5–2.5 mm long, glabrous or sparsely appressed pubescent; corolla white or white and deeply suffused with rose or pink, the tube cylindric, 6–8 mm long, 2–4 mm in diameter, glabrous internally and glabrous to sparingly appressed pilose externally, the lobes 4, erect to horizontally spreading, ca. 1 mm long, deltoid, acute; stamens 8, about as long as the corolla, the filaments 3.5–5 mm long, flattened moderately to densely hyaline setose, the anthers slightly granular, ca. 1.5–2 mm long, each theca tapering into a slender tubule 2.5–3.5 mm long, style glabrous, slightly exserted beyond the corolla lobes.

As is suggested by the description, there is much variability in this species and yet none of it merits formal recognition. *Disterigma humboldtii* is known from Guatemala, Costa Rica, Panama (Bocas del Toro, Chiriquí and Veraguas) and northern South America.

BOCAS DEL TORO: Róbalo Trail, northern slopes of Cerro Horqueta, 6000–7000 ft, *Allen 4986* (F, MO, US). CHIRIQUÍ: Bajo Mono-Róbalo Trail, W of Cerro Horqueta, 5000–7000 ft, *Allen 4845* (F, MO, NY, US). Bajo Chorro, Boquete District, 6000 ft, *Davidson 92* (F, MO). Upland pastures, Las Nubes, 7200 ft, *Luteyn 3039* (DUKE). Valley of the upper Río Chiriquí Viejo, *White 25* (MO). Bajo Chorro, 1900 m, *Woodson & Schery 633* (MO, NY), *684* (MO, NY). VERAGUAS: Cerro Tute, ca. 10 km NW of Santa Fé, on ridgetop in cloud forest above 1000 m, *Mori et al. 7597* (MO).

2. **Disterigma luteynii** Wilbur, Bull. Torrey Bot. Club 101: 248. 1974. TYPE: Panama, Panamá, Cerro Jefe, *Luteyn 3206* (DUKE, holotype; F, MO, isotypes).

Straggly, scrambling epiphytic *shrub* with branches to 4–6(–10) dm long; branchlets terete, moderately to densely spreading puberulous with hyaline, sordid or tawny trichomes ca. 0.2 mm long; internodes mostly 1–2 mm long but occasionally 3–5 mm. *Leaves* coriaceous, entire, narrowly oblanceolate, or elliptic, 8–12 mm long, 2.5–4.5 mm wide, mostly about 3 times as long as wide,

apically acute in general outline but the actual apex obtuse, gradually tapering basally into the petiole, moderately to densely appressed to spreading pubescent with inconspicuous, fine, hyaline trichomes less than 0.1 mm long on both the surfaces, the lower surface also with a sparse scattering of dark clavate glands, the midvein distinctly impressed above, slightly elevated beneath and the venation otherwise indistinct above and indefinite but pinnately parallel below, dark green above and green below; petioles 1–1.5 mm long, moderately spreading short pubescent with sordid trichomes, conspicuously glaucous. *Inflorescence* of solitary, subsessile flowers; pedicels to 1.2 mm long; bracts 2–3, basal, oblong to ovate, pale green; bracteoles 2, broadly clasping, ovate, broadly rounded, borne just beneath and embracing the flower, outside moderately to densely spreading fine pubescent, glabrous within. *Flowers* with the hypanthium terete, campanulate, glabrous, pale green, 0.5–0.7 mm long, 1.2–1.5 mm in diameter; calyx lobes 4, erect to slightly spreading, deltoid, acute, 1.5–1.7 mm long entire and ciliate, sparsely and very finely pubescent externally; corolla white with pinkish hue, the tube cylindric, 4–5 mm long, 1.8–2.2 mm in diameter, glabrous, the lobes 4, strongly spreading, the recurved tips ca. 1.5 mm long, deltoid, acute with strongly incurved margins; stamens 8, exserted beyond the corolla tube and only a little shorter than the lobes, the filaments white, 2–2.2 mm long, flattened, moderately to densely hyaline setose, the anthers red, minutely granular papillate, ca. 1 mm long, each thecae tapering into a slender tubule ca. 2 mm long; style pale green, glabrous, exserted slightly beyond the corolla lobes.

Disterigma luteynii is only known from the Cerro Jefe region of central Panama.

PANAMÁ: Lowland cloud forest around the summit of Cerro Jefe, ca. 1000 m, *Luteyn 3206* (DUKE, F, MO). Along the road and at the top of Cerro Jefe, ca. 3000 ft, *Luteyn & Kennedy 3950* (DUKE, MO, NY). Cloud forest at top of Cerro Jefe, *Mori & Kallunki 2382* (MO). Premontane rainforest, Cerro Jefe, ca. 1000 m, *Mori & Kallunki 3610* (MO). Disturbed cloud forest on top of Cerro Jefe, 1000 m, *Nee 13971* (MO). Cerro Jefe in Clusia forest at 2700–3000 ft, *Tyson et al. 3266* (SCZ).

3. **Disterigma panamense** Standley, Fieldiana Bot. 22: 365. 1940. TYPE: Panama; *Terry 1564* (F, holotype).

Straggly epiphytic *shrub* 2–10 dm tall; brachlets subterete, irregularly ridged and grooved, moderately to densely spreading pilosulose with hyaline to slightly tawny trichomes mostly 0.3–0.7 mm long; internodes short, mostly less than ⅓ the length of the nearest leaf and usually 2–7 mm long. *Leaf blades* coriaceous, strongly spreading or merely divergent forming an angle 90°–45°; minutely and indistinctly serrulate or entire, typically narrowly linear oblong to elliptic, less commonly shortly and narrowly oblanceolate, mostly 8–12 mm long, 2.5–4 mm wide, typically about 4-times as long as wide, apically acute, basally tapering or somewhat rounded, sparsely and indistictly appressed pilosulose, especially on the lower surface, becoming glabrate, obscurely and finely short ciliate near the apex but becoming glabrate; venation obscure, neither elevated nor impressed; petioles 1–1.5 mm long, moderately to densely spreading puberulous or short pubescent, the trichomes 0.2–0.5 mm long. *Inflorescences* of solitary,

subsessile flowers; bracts 2–3, basal, broadly clasping, ovate, ciliate, almost as broad as long; bracteoles 2, broadly clasping, ovate, sparsely puberulous, ciliate, 2.5–3.5 mm long, borne just beneath and embracing base of the flower. *Flowers* with the hypanthium terete in cross section, campanulate, glabrous, ca. 1 mm long, 1 mm in diameter; calyx lobes 4, acute, erect, lance ovate, 2–2.5 mm long, entire, conspicuously ciliate with spreading, hyaline trichomes ca. 0.2 mm long, sparsely appressed pilosulose or glabrous; corolla white, glabrous, the tube cylindric, 4–6 mm long, 1.5–2.5 mm in diameter, glabrous, the lobes 4, acute, triangular, erect; stamens equalling the corolla and the style. *Berry* white, thin walled, many seeded.

Disterigma panamense is known only from two collections both made in the mountains of Darién.

DARIÉN: Cuasí-Caná Trail between Cerro Campamiento and La Escaler to "Paramo" east of Tres Bocas, *Kirkbride & Duke 1282* (MO, NY). Caná-Cuasí Trail, 5500 ft, *Terry & Terry 1564* (F).

4. **Disterigma trimerum** Wilbur & Luteyn, Brittonia 29: 258. 1977. TYPE: Panama, *Wilbur & Luteyn 19321* (DUKE, holotype; CAS, DUKE, F, GH, MICH, MO, NY, PMA, US, isotypes).

Epiphytic or terrestrial, bushy *shrubs* 0.5–1.5(–2) m tall; branchlets sharply ridged and grooved, indistinctly 3-angled to irregularly 4-angled, glabrous, sparingly strigillose or minutely puberulent; mature branches becoming terete, grayish to blackish, conspicuously fissured; internodes ⅕–⅗ as long as the surrounding leaves. *Leaf blades* coriaceous, entire to obscurely and microscopically serrulate, broadly elliptic to somewhat obovate or spatulate, (0.8–)1.2–1.8 cm long, (4–)6–12 mm wide, apically obtuse to broadly rounded, basally cuneate, glabrous above, beneath evenly but sparingly beset with appressed, amber colored trichomes 0.2–0.3 mm long; midvein and the principal veins slightly elevated above to nearly plane, beneath the midvein and the 1–2 pairs of paralleling principal veins plane or slightly elevated, dark green above, pale green beneath; petioles 3–5 mm long, glabrous, flattened above. *Inflorescence* of solitary, axillary, subsessile flowers; pedicles disarticulating apically, 2–3 mm long; bracteoles subopposite, broadly clasping, semiorbicular, ciliate, 1.5–1.8 mm below the base of the calyx tube, ca. 1.5 mm long, 1.8–2.0 mm wide, scarcely overlapping the base of the hypanthium; bracts 1–3, deltoid to acutely oblong, situated near the base of the pedicel. *Flowers* with the hypanthium terete, short, cylindric, glabrous, ca. 3.5 mm long, 2.0–2.2 mm in diameter; calyx lobes 3, erect, broadly deltoid, acute, ca. 0.5 mm high, entire, eciliate, glabrous; corolla deep red, thinly fleshy, the tube cylindric, abruptly tapering into a basal portion 2.0–2.3 mm long, 1.0–1.4 mm in diameter, the longer portion of the tube 5.0–5.5 mm long, ca. 2.5 mm in diameter, trichomes few, ascendent, 0.1–0.2 mm long, the lobes 3, erect, 1.5–2.0 mm long, 1.0–1.2 mm wide, acute, oblong deltoid; stamens 6, ca. 1 mm shorter than the corolla tube, the free portion of the filaments ca. 2.5 mm long, flattened, glabrous, the anthers granular, 2.5–2.8 mm long, each theca tapering into a slender tubule 2.5–2.8 mm long, dehiscing by an introrse, elongate, oval slit ca. 1.5 mm long; style glabrous, slender, ex-

tending 1.0–1.2 mm beyond the stamens or to the top of the corolla tube. *Berry* at first greenish white turning dark blue.

Except for this species, trimerous flowers are not known in *Disterigma*. The deep red corollas of *D. trimerum* are unlike those of any other Central American representative of the genus. *Disterigma trimerum* is endemic to western Panama.

CHIRIQUÍ: Cloud forest on Caldera-Chiriquicito Trail between Q. Hondo and divide, *Kirkbride & Duke* 939 (DUKE). Heavily forested slopes along W side of Cerro Horqueta, 1700–1800 m, *Luteyn 3750* (DUKE, NY). Premontane cloud forest along ridge E of Cerro Horqueta, 1700–1900 m, *Luteyn & Wilbur 4611* (DUKE, NY, US). Cerro Hornitos, 40 km NW of Gualaca, cloud forest dominated by *Quercus*, *Podocarpus* and *Drimys* 2238 m, *Mori & Bolton 7470* (DUKE, MO). Slopes approaching Cerro Horqueta 6.6 km NNE of Boquete, 1500–1800 m, *Wilbur & Luteyn 19321* (CAS, DUKE, F, GH, MICH, MO, NY, PMA, US).

5. **Disterigma utleyorum** Wilbur & Luteyn, Brittonia 29: 259. 1977. TYPE: Costa Rica, *Wilbur 21706* (DUKE, holotype; CAS, CR, F, GH, LL, MICH, MO, NY, PMA, WIS, etc. isotypes).

Epiphytic *shrub* 2–4.5 dm tall; branchlets subterete to terete, moderately to densely scurfy puberulent; internodes short and mostly ⅓–⅔ as long as the nearest leaf. *Leaf blades* oblong obovate, somewhat spatulate or rarely oblong elliptic, thick and fleshy, wrinkled when dried, apically obtuse to broadly rounded and often with a pointed apiculus 1–2 mm long, basally broadly cuneate to obtuse, (1.0–)1.5–2.5(–3.0) cm long, (0.7–)1–1.8 cm wide, entire and slightly revolute, both the surfaces minutely or even microscopically puberulent and also with amber colored strigillose trichomes ca. 0.1 mm long; venation with 5 prominently elevated veins radiating from the petiole; petioles 1–2(4) mm long, 1–1.2 mm wide, short puberulent. *Inflorescences* solitary flowers in the axils of the upper leaves, subsessile; pedicels 1–2 mm long, bracts 2, subopposite, broadly oblong to ovate, loosely clasping, minutely appressed puberulous, 1.5–2 mm long, 2–3 mm wide, fused below into a cupule 0.5–1 mm long. *Flowers* with the hypanthium cylindric, 2–3 mm long, pale green, finely and minutely puberulous; calyx rim 1–1.2 mm high, the lobes 4, erect, lanceolate to narrowly triangular, acute, 1.6–2.2 mm long, ca. 1 mm wide at base, minutely puberulous; corolla white, cylindrical or barrel-shaped to somewhat funnelform at maturity, glabrous to sparingly spiculate, the tube 4–5.5 mm long, 3.5–4 mm in diameter, the lobes 4, oblong elliptic, acute, 3.5–5 mm long, about 3 mm wide; stamens 8, ca. 5 mm long, just a little shorter than the corolla tube at anthesis, the filaments white, sparingly ciliate, 1.5–2.5 mm long, the anthers smooth, 2.5–3.5 mm long, the 2 thecae emptying into a single orange tubule 1.5–2.0 mm long which opens by a single, more or less terminal, obliquely introrse, circular pore; style glabrous, 4.8–5.3 mm long, 0.6–0.8 mm in diameter; stigma slightly bilobed. *Berries* reportedly "translucent white."

This species is known only from recently collected specimens made at low montane elevations from Panama, Costa Rica, Colombia and Ecuador. This species seemingly is always intimately associated with a large colony of ants which vigorously defend their home. The specimens seen by us formed a

picket fence surrounding a large, moist ball of earth and vegetable debris a foot or so in diameter capped by a dense, mat-forming, acrocarpus moss. Details of the commensal relationship between ericad and insect are at present unknown.

VERAGUAS: 5 mi W of Santa Fé on road past Escuela Agrícola Alto Piedra on Pacific side of divide, 800–1200 m, *Liesner 942* (MO).

8. GAULTHERIA

Gaultheria L., Sp. Pl. 1: 395. 1753; Gen. Pl., ed. 5. 187. 1754. TYPE: *G. procumbens* L.

Chiogenes Salisb., Trans. Hort. Soc. London 2: 94. 1817. TYPE: *C. serpyllifolia* Salisb. = *G. hispidula* (L.) Muhl.

Upright terrestrial or epiphytic *shrubs*, prostrate *undershrubs* or rarely small *trees*. *Leaves* persistent, short petiolate, usually serrate, pinnately veined. *Inflorescences* terminal panicles, axillary racemes or rarely solitary in the axils of the leaves; pedicels clearly articulated or jointed below the flower; bracteoles 2 or several, basal, medial or closely subtending the pedicels. *Flowers* with the calyx (4)5-parted, usually accrescent and becoming somewhat fleshy; corolla campanulate to urceolate, white to pinkish or reddish; stamens (8)10, the filaments distinct, basally expanded, borne on the base of the corolla, the anthers with white tissue on the abaxial side and often with 2, ascendent, terminal awns on each anther sac which open introrsely by a single apical pore; stigma obtuse or truncate, the style straight, the ovary superior or rarely partly inferior, (4)5-locular, ovules 5–10 (or many). *Fruit* a (4)5-valved, loculicidal capsule enclosed by the usually colored, slightly to conspicuously fleshy calyx and thus sometimes appearing superficially berrylike; seeds usually numerous, small, angled, and wingless.

Gaultheria is a genus of 150 species widespread in temperate regions and extending into the montane tropics. It occurs in both northern and southern hemispheres and in both the New and the Old World.

Neither Williams' (1965) attempt to deal with the genus in Guatemala nor ours in southern Central America has satisfactorily resolved the large number of problems associated with the genus in Mexico and Central America; the resolution of problems in the genus in this area clearly demands an intensive study from throughout at least this range.

We find ourselves very sympathetic to the findings of Williams (Fieldiana Bot. 31: 169–172. 1965.) that ". . . the characters which have been used to segregate species in this genus are not impressive and . . . are obviously subject to variation which is almost endless" and "one begins to wonder if perhaps the systematics of the group may not have degenerated to the naming of specimens rather than . . . biological units."

a. Leaves elliptic to lance elliptic, (1–)1.5–2.5(–3.4) cm wide, usually (2.5) 3-times as long as wide ..... 1. *G. gracilis*
aa. Leaves broadly elliptic to oblong elliptic to oblong, (1.5–)2.5–4.0(–5.5) cm wide, usually less than 2.5-times as long as wide ..... 2. *G. odorata*

1. **Gaultheria gracilis** Small, N. Amer. Fl. 29: 77. 1914. TYPE: Costa Rica; La Palma, *Tonduz 7463* (US, holotype).—FIG. 8.

G. barbata Small, N. Amer. Fl. 29: 77. 1914. TYPE: Costa Rica; Volcán Poás, *Pittier 2051* (US, holotype).
G. setosa Small, N. Amer. Fl. 29: 77. 1914. TYPE: Panama; *Pittier 3245* (US, holotype).
G. gracilis var. *intermedia* Suessenguth & Goeppinger, Bot. Jahrb. Syst. 72: 282. 1942. TYPE: Costa Rica, *Kupper 889* (M). Invalid, Latin diagnosis not provided.

Shrubs 0.4–1.0 m tall, epiphytic or terrestrial; branches terete with brown, grayish or blackish, often fissured bark; branchlets terete, usually moderately to densely strigose with slender, antrorsely appressed, sharply pointed, often hyaline trichomes mostly 0.5–2.5 mm long, occasionally moderately to densely barbate with slender, strongly ascendent to divergently spreading, sharply pointed, golden brown to dark brown trichomes 1–4(–5) mm long, rarely glabrate. *Leaf blades* coriaceous, elliptic to lance elliptic, mostly (3–)4–6(–8.5) cm long, (1–)1.5–2.5(–3.4) cm wide, basally cuneate to rounded, apically acuminate to acute, minutely and indistinctly serrulate, the serrations often tipped by a slender, appressed bristle 1.0–2.2 mm long, above with sparce to plentiful appressed, slender trichomes (0.5–)1.0–2.0 mm long, these often deciduous, their often reddish bases appearing as punctate glands, beneath usually more obviously and densely appressed setose, the slender, golden to reddish brown trichomes (1–)2–3 mm long; venation pinnate, the lateral veins strongly arching towards the apex, the connecting veins forming a conspicuously elevated reticulate pattern, usually less conspicuously so above; petiole subterete or somewhat flattened and grooved adaxially, warty or papillate, drying somewhat wrinkled, short pubescent or glabrate, often strigillose with trichomes 1.0–2.5 mm long, mostly 4–6 mm long, 1.0–1.5 mm in diameter. *Inflorescence* a raceme arising from the axils of the upper leaves; rachis irregularly ridged and grooved or terete, typically moderately to densely puberulent with soft, white trichomes, (2–)3–7(–8) cm long, ca. 1 mm in diameter; floral bracts persistent, membranous to papyriferous, broadly elliptic to spatulate, somewhat cucculate, usually strongly divergent from the rachis, mostly 3–10(–14) mm long, 2–6 mm wide, markedly striate, ciliate and occasionally distally glandular fimbriate, thinly microscopically puberulous on both the surfaces or glabrous, white or greenish white to roseate; pedicels terete, finely striate, usually strongly divergent, but moderately to densely fine puberulous, 5–10(12) mm long, 0.4–0.6 mm in diameter; bracteoles 2, more or less alternate and borne variably in the median half of the pedicel, usually strongly divergent, papyraceous, linear to narrowly oblong, 2.0–4.5 mm long, 0.5–1.0 mm wide, minutely ciliate, creamy or greenish white to roseate. *Flowers* with the calyx sharply demarcated from the pedicel by a groove, the tube smooth, shallowly campanulate, 1.4–2.0 mm long, 2.2–3.5 mm in diameter, broadly rounded basally, the lobes 5, erect, ovate to deltoid, apically acute to acuminate, mostly 2.0–3.0 mm long, basally 1.8–2.5 mm wide, ciliate, the sinuses acute; corolla urceolate to conical, 4–8 mm long, about 3.0–4.0 mm in diameter just above the base, tapering above to 1.8–2.2 mm in diameter just below lobes, greenish, white to deeply roseate; moderately to sparsely beset with hyaline to golden tawny, strigillose trichomes 0.2–0.6 mm long, the lobes oblong to triangu-

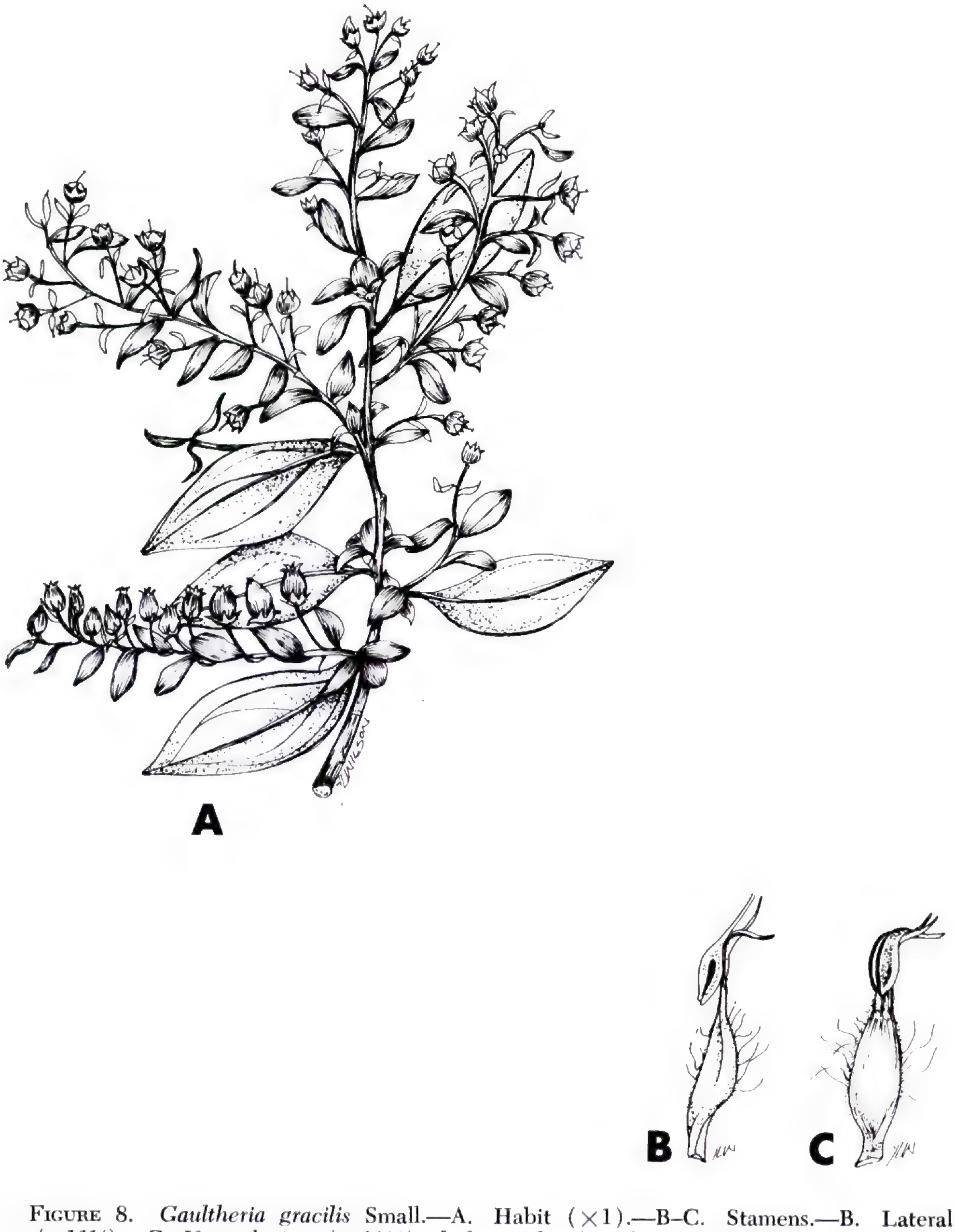


FIGURE 8. *Gaultheria gracilis* Small.—A. Habit (×1).—B–C. Stamens.—B. Lateral view (×11⅕).—C. Ventral view (×11⅕). [After *Utley & Utley 3718* (DUKE), Costa Rica.]

lar, 1.0–1.5 mm long, slightly spreading to somewhat reflexed at maturity; stamens 10, the filaments distinct, finely papillate, 1.5–2.2 mm long, white, the thecae finely granular, 1.0–1.2 mm long, dehiscing by an introrse terminal cleft, each anther sac terminated by 2 extrorsely deflexed awns ca. 0.5 mm long; stigma truncate, the style persistent, glabrous, 2.5–4 mm long, the ovary 5-celled, subglobose, usually glabrous. *Fruit* a 5-celled capsule 2.5–4 mm high, 3.5–5 mm in diameter.

Within the past six decades five or more additional species have been recognized in Panama and Costa Rica based solely upon differences in type and abundance of the pubescence on both vegetative and floral organs. *Gaultheria setosa* appears to be no more than one extreme of a continuum ranging from glabrous to almost densely strigillose corollas. Much of this morphological range can be found in any given population or from the duplicates collected from a sizable population. Instead of strigose twigs or branchlets, *G. barbata* is characterized by a dense covering of strongly spreading trichomes which give those plants so provided a strikingly different appearance. Plants have been found however which have both types of pubescence although on different branches. Other plants are found which blur the sharp distinction between strigose and hirsute by representing a wide range of intermediate states. In fact *Gaultheria gracilis* var. *intermedia* Suessenguth & Goeppinger was proposed as intermediate between *G. gracilis* and *G. barbata*. *Gaultheria gracilis* is endemic to Costa Rica and western Panama.

CHIRIQUÍ: Lower montane rain forest on W-facing slopes of south flank of Cerro Horqueta, 1940–2000 m, *Cochrane et al. 6268* (F, MO). Premontane rainforest along ridge to the top of Cerro Horqueta, *Luteyn 3077* (DUKE, NY). Cerro Pando, ca. 16 km NW of El Hato del Volcán, 2000–2482 m, *Mori & Bolten 7299* (DUKE, MO). Humid forest around Las Siguas Camp, S slope of Cerro de la Horqueta, ca. 1700 m, *Pittier 3245* (US). Southern slopes of Cerro Horqueta N of Boquete, 6400–6600 ft, *Wilbur et al. 13448* (DUKE, F, MO, NY, PMA). S slopes of Cerro Horqueta N of Boquete, 7000 ft, *Wilbur et al. 13468* (DUKE, F, GH, MICH, MO, NY, PMA, US).

2. **Gaultheria odorata** Willd., Ges. Naturf. Freunde Berlin Neue Schriften 3: 425. 1801. TYPE: Caracas, Venezuela, *Humboldt* in Herb. Willd. (B, not seen, presumably destroyed).

G. odorata var. *costaricensis* Donnell Smith, Bot. Gaz. (Crawfordsville) 20: 292. 1895. TYPE: Costa Rica; Cartago, Estrella, *Cooper 5841* (US, lectotype; F, MO, NY, US isotypes).
G. costaricensis (Donnell Smith) Small, N. Amer. Fl. 29: 79. 1914.
G. glandulifera Small, N. Amer. Fl. 29: 78. 1914. TYPE: Costa Rica; Volcán Poás, *Donnell Smith 6639* (NY, holotype; GH, US isotypes).
G. donnellii Sleumer, Notizbl. Bot. Gart. Berlin-Dahlem 12: 125. 1934. TYPE: Costa Rica; Laguna de Barba, *Hoffmann 3* (B, holotype, not seen; fragment of holotype, US).
G. poasana Sleumer, Notizbl. Bot. Gart. Berlin-Dahlem 12: 127. 1934. TYPE: Costa Rica; Volcán Poás, *Donnell Smith 6631* (B, holotype; NY, US isotypes).
G. chiriquensis Camp, Ann. Missouri Bot. Gard. 27: 328. 1940. TYPE: Panama; *Allen 1542* (NY, holotype; MO, US isotypes).

Shrubs mostly 0.5–1.2(–2.0) m tall, terrestrial or rarely epiphytic; branches terete with reddish, reddish brown or grayish, often fissured bark; branchlets terete, extremely varied as to pubescence, often moderately to densely puberulous, hispid with strongly spreading, bristly trichomes to 5 mm long, these often gland tipped, sometimes glabrate. *Leaf blades* coriaceous, broadly elliptic, oblong elliptic to oblong, mostly (3–)5–9(–11) cm long, (1.5–)2.5–4.0(–5.5) cm wide, basally rounded, often broadly so, sometimes cuneate, rarely cordate, apically acute to rounded, often with an abruptly acute tip, shallowly and often indistinctly serrulate, the serrations commonly tipped when young by slender, caducous, setose bristles 0.8–1.2 mm long, the upper surface often glabrous except

for the inconspicuous puberulence in the grooves of the impressed principal veins, occasionally sparingly to moderately beset with erect to strongly ascendent, usually gland tipped bristles 0.3–0.6 mm long, their former presence marked by a reddish punctation, the lower surface sparingly to moderately beset with ascendent, often gland tipped, reddish brown or golden brown trichomes 0.1–0.8 mm long; venation pinnate, the principal veins impressed above and somewhat elevated beneath, the secondary veins strongly arching towards the apex, tertiary and other connecting veins reticulate, visible on both the surfaces; petioles subterete, somewhat flattened and grooved adaxially, often drying wrinkled, often puberulous especially in the adaxial groove, occasionally sparingly to moderately hispid, the bristly trichomes to 2–3 mm long and occasionally gland tipped, occasionally glabrate, mostly 4–12 mm long, 1.5–3.0 mm in diameter. *Inflorescences* racemes arising from the axils of the upper leaves, often aggregated so as to appear densely paniculate; rachis strongly ridged and grooved to terete, mostly (4–)6–10(–12) cm long, 1.0–1.5 mm in diameter, moderately to densely puberulent but often with additionally sparse to dense gland tipped bristles 0.6–1.2 (–2.0) mm long; floral bracts persistent, papyriferous, elliptic to elliptic oblong, oblanceolate or spatulate, somewhat cucculate, usually strongly divergent from rachis, mostly 5–15(–18) mm long, 3–8(–10) mm wide, conspicuously striate, ciliate and usually glandular fimbriate distally, often moderately to densely but inconspicuously puberulous and glabrescent, occasionally sparingly to densely beset with gland tipped bristles externally, greenish white or stramineus to pinkish or roseate; pedicels terete but finely striate, usually strongly divergent, moderately to densely puberulous, occasionally with gland tipped bristles 0.5–1.0 mm long, mostly (5–)8–12 mm long, ca. 0.5 mm in diameter; bracteoles 2, opposite or subopposite, usually borne medially or in the lower half of the pedicel, typically strongly divergent at anthesis, membranous, linear to narrowly elliptic or lanceolate, mostly 3–6 mm long, 0.6–1.2 mm wide, usually whitish puberulous externally and often internally as well, occasionally with reddish, gland tipped bristles 0.2–0.5 mm long, greenish white, stramineous or roseate. *Flowers* with the calyx sharply delineated from the pedicel by a groove, the tube shallowly campanulate, 1.5–2.0 mm long, 2.5–3.2 mm in diameter, broadly rounded basally, the lobes 5, erect, lance ovate to deltoid, apically acute to acuminate, mostly 2.0–3.5 mm long, basally 2.0–2.8 mm wide, ciliate, externally moderately to densely puberulent, occasionally sparingly to densely beset with gland tipped, hirsute trichomes 0.2–0.5 mm long; corolla pentagonally conical to urceolate, moderately to densely hyaline puberulous and occasionally with appressed to spreading, gland tipped, hirsute bristles 0.3–1.0 mm long, 4–8 mm long, 3.0–4.0 mm in diameter just above the base, tapering above to 2–3 mm in diameter, usually roseate, the lobes oblong to deltoid, acute, 1.2–1.6 mm long, spreading to somewhat reflexed at maturity; stamens 10, the filaments distinct, ciliate and also papillate, ca. 2 mm long, white, the thecae finely granular, 1.0–1.2 mm long, dehiscing by an introrse terminal cleft, each anther sac terminated by 2 extrorsely deflexed awns 0.3–0.5 mm long; stigma truncate, the style persistent, usually short puberulous, 3–4 mm long, the ovary 5-celled, subspherical, usually short pubescent. *Fruit* a 5-celled capsule 3–4 mm high, 3.5–4.5 mm in diameter.

Variation encountered within the *Gaultheria odorata* complex resembles that of the *G. gracilis* complex in that it is largely based on type and distribution of pubescence types, but there is more variation in leaf shape in the *odorata* complex than in the *gracilis* complex. *Gaultheria chiriquensis* Camp with its crispy pilose branchlets and conspicuously cordate leaves is the most distinctive element to be segregated. The names *G. odorata s.s.*, *G. costaricensis*, and *G. donnellii* are based on plants which all occur in the same general area as *G. chiriquensis* and intermediate specimens have been seen. For the present it is wisest to recognize *G. odorata* as an extremely polymorphic species ranging from southern Mexico into northern South America.

CHIRIQUÍ: Llanos on slopes of Volcán de Chiriquí along Río Chiriquí Viejo, 1200 m, *Allen 1004* (MO, NY). Llanos del Volcán, 1300 m, *Allen 1542* (MO, NY). Llano del Volcán, 1500–1600 m, *Allen & Fairchild 3462* (US). Summit and SW face of Cerro Copete, 9000 ft, *Allen 4882* (MO, US). Slopes of Las Cumbres near Cerro Punta, *Croat 13757* (DUKE, MO). Lava flow between El Hato and Bambito, *D'Arcy 10027* (MO). Top of peak between Barú and Respinga, 3000 m, *D'Arcy 10085* (MO). Roadside, Potrero Muleto to summit of El Barú, *D'Arcy 10168* (MO). Elfin forest on ridges above Potrero Muleto, W slope of Volcán de Chiriquí, 11 km WNW of Boquete, *Davidse & D'Arcy 10249* (DUKE, MO, NY). Lava flow 3 km NE of El Hato del Volcán at base of Barú, *Davidse & D'Arcy 10347* (DUKE, MO, NY). Bajo Chorro, Boquete District, 5000 ft, *Davidson 391* (MO, US). Potrero Muleto, 10500 ft, *Davidson 1019* (F, US). Exposed rocky summit, Piedro de Lino, 1900 m, *Killip 3574* (US). Llanos outside of El Hato del Volcán, 6000 ft, *Luteyn 3051* (DUKE, NY). Barú, 2900 ft, *McCorkle c158* (FSU, SCZ). Moist summit of Cerro de Lino above Boquete, 1560 m, *Maxon 5210* (US). Elfin forest on E side of Volcán Barú, 3000 m to just below summit, *Mori & Bolten 7429* (DUKE, MO). Lava flow on W slopes of Barú, 1500 m, *Mori & Kallunki 5693* (MO). Trail to summit on western slopes of Volcán de Chiriquí, 2500–3400 m, *Mori & Kallunki 5756* (MO). Savanna 1 mi S of Bambito, 1600 m, *Partch 69-21* (F). Forests of Cerro Lino above Boquete, 1300–1560 m, *Pittier 3032* (NY, US). Near peak, Volcán de Chiriquí, 11200 ft, *Terry 1310* (F). Dry windswept canyon, 8 mi NE of El Volcán, 8100–8400 ft, *Tyson 837* (FSU). Lava flow 5 mi above Volcán, 4900 ft, *Tyson 7293* (PMA). West slope of El Barú, 10000–11000 ft, *Tyson & Loftin 6148* (DUKE). W slope of El Barú above 11000 ft, *Tyson & Loftin 6154* (DUKE, FSU). Lava flow NE of El Hato del Volcán near Aguacate, 1800–1900 m, *Wilbur et al. 10975* (DUKE, MO, NY, PMA). W slopes of Volcán de Chiriquí, 9800 ft, *Wilbur et al. 11028* (DUKE). Lava field 5 mi NE of El Hato del Volcán, *Wilbur et al. 11862* (DUKE, MO). Lava field 4 mi NE of El Hato del Volcán near Río Macho del Monte, 1800 m, *Wilbur et al. 13068* (DUKE, MO, PMA). Rocky arroyo on lava field 4.2 km N of El Hato del Volcán, 1400–1600 m, *Wilbur & Luteyn 19412* (DUKE).

9. LATEROPORA

Lateropora A. C. Smith, Contr. U.S. Natl. Herb. 28: 333. 1932. TYPE: *Lateropora ovata* A. C. Smith.

Terrestrial or epiphytic *shrubs*. *Leaves* alternate, petiolate, pinnately veined, coriaceous. *Inflorescences* axillary, compact, umbelliform or racemose, the stout, short pedicels each subtended by a persistent, ovate bract and bearing basally a pair of subopposite, persistent, ovate bractlets. *Flowers* with the hypanthium clearly disarticulating from the pedicel by a conspicuously delineated groove fringed with apparently glandular, minute trichomes, coriaceous, campanulate; calyx lobes 5, triangular, erect; corolla thick walled, broadly urceolate or squatly campanulate, densely pilose within, the lobes 5, triangular, reflexed; stamens 10, nearly as long as the corolla tube, the filaments distinct, weakly adherent to the base of the corolla, pilose especially near the connective, the anther attached

slightly below the middle, the anther sacs granular, strongly basally incurved with the lower ⅓ protruding inwardly or even turning upward, spurs and awns lacking, tubules small and rudimentary, the thecae dehiscing by lateral clefts extending from the apex to approximately the base; the base strongly curved; stigma truncate, the style filiform, the ovary inferior, 5-locular. *Fruit* a berry.

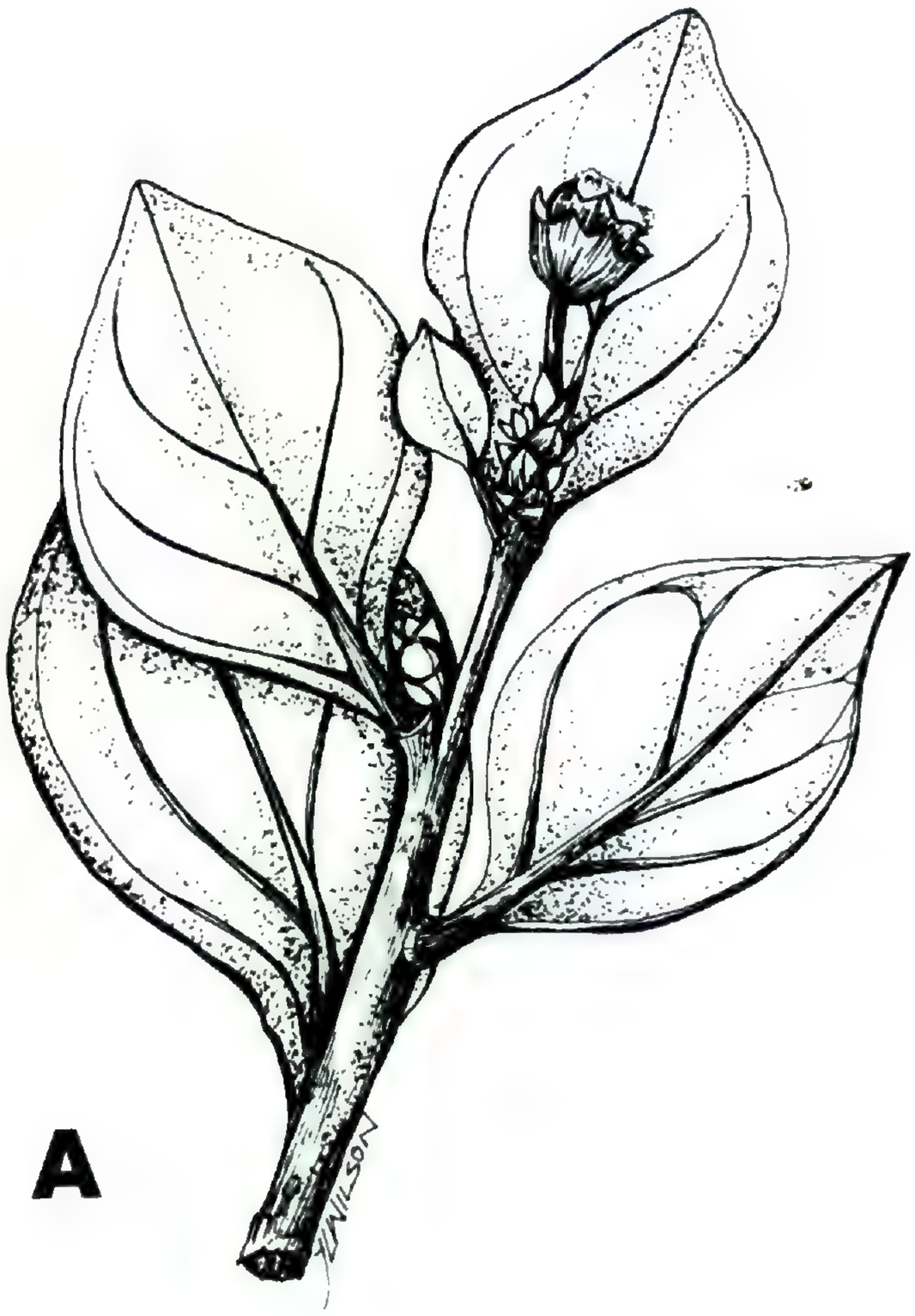
Lateropora is a genus of two species known only from Panama.

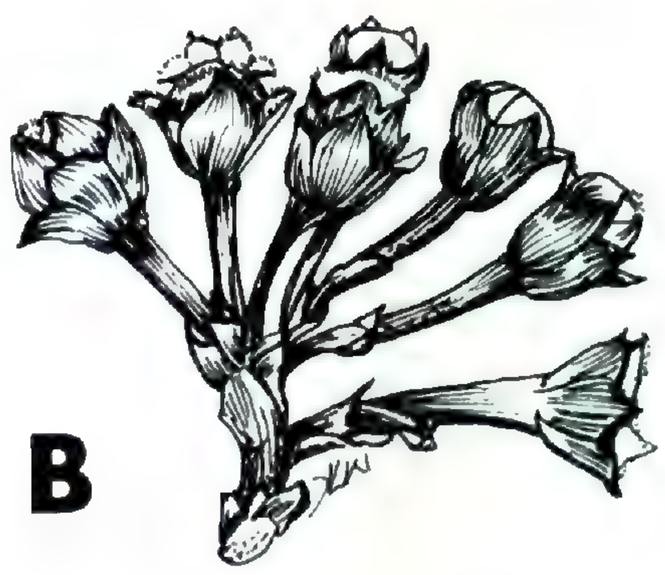
a. Calyx lobes 2–3 mm long and 4–5 mm wide basally; corolla lobes ca. 3 mm long and 4.5–5.0 mm wide basally; petioles 5–15 mm long; Chiriquí Province ..... 1. *L. ovata*
aa. Calyx lobes 1.5–2 mm long and 2.0–2.2 mm wide basally; corolla lobes 1.5–1.8 mm long and 2 mm wide basally; petioles 3–5 mm long; Veraguas Province .. 2. *L. santafeënsis*

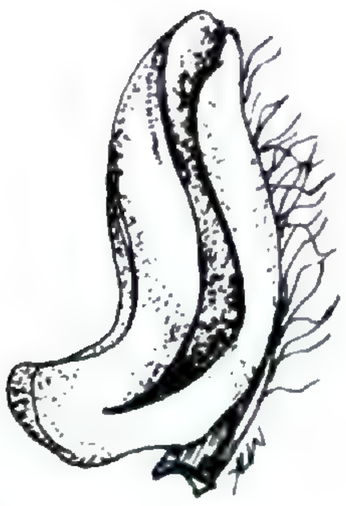
1. **Lateropora ovata** A. C. Smith, Contr. U.S. Natl. Herb. 28: 334. 1932. TYPE: Panama: *Pittier 3234* (US, holotype; photo of holotype, DUKE, NY).—FIG. 9.

Epiphytic or terrestrial *shrub*, 2–3 m tall; branches and branchlets subterete, glabrous, striate, thick and widely divergent. *Leaf blades* coriaceous, ovate to broadly elliptic, 6–13 cm long, 4–6(–9) cm wide, glabrate or with appressed, reddish brown, strigillose trichomes 0.2–0.6 mm long, basally cuneate, acute to obtuse apically, entire, pinnately veined, the 3–5 secondary veins arcuate and the veinlets conspicuously reticulate, slightly elevated both above and beneath; petioles glabrous, 0.5–1.5 cm long, 1.5–3 mm in diameter. *Inflorescences* compact axillary, umbelliform racemes, the glabrous, stout peduncle and rachis 12–16 mm long, basally bracteate, the broadly ovate, thick, scale-like, ciliate bracts 4–5 mm long, 3.5–4.5 mm wide subtending the pedicels, the pedicels 3–10 mm long, 2 mm in diameter, bracteoles 2, subopposite, broadly ciliate, keeled, ovate, 3–4 mm long, 4–5 mm wide borne near the base of the pedicel. *Flowers* with the hypanthium disarticulating from the pedicel by a marked groove and with a fringe of glandular trichomes 0.1–0.2 mm long, campanulate, thick walled, 4–5 mm high, 4 mm in diameter, sparingly strigillose with appressed glandular trichomes; the limb glabrous, 1–1.5 mm high, the lobes erect or incurved, broadly triangular, acute, 2–3 mm long, 4–5 mm wide basally, short ciliate; corolla tube broadly cylindric or subglobose, pale greenish white, 6–8 mm long, medially 7–8 mm in diameter, sparsely pubescent outside near the middle with appressed trichomes 0.4–0.6 mm long, the lobes spreading to reflexed, triangular, acute, ca. 3 mm long, 4.5–5 mm wide at the base, densely tangled villous within with white trichomes 0.4–0.7 mm long; stamens 10, the filaments flattened, 3–4 mm long, broadened basally to ca. 1 mm wide, tapering gradually upwards to ca. 0.6 mm, glabrous for about the basal third, strikingly pilose above with trichomes 0.5–1 mm long, the anthers medially attached, conspicuously granular, 3–4 mm long, the tubules submembranous, vestigial to 0.3 mm long, the base strongly incurved, ca. 1 mm long, the thecae dehiscing by a longitudinal slit extending from the apex to the base, basally with a pronounced curve; style ca. 7 mm long.

This little known species has been collected only from the vicinity of Boquete on the slopes of Cerro de la Horqueta. It is apparently restricted to the higher and wettest ridges and slopes.







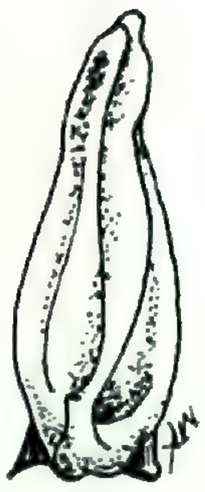


FIGURE 9. *Lateropora ovata* A. C. Smith.—A. Habit (×1⅕).—B. Inflorescence (×1⅕).—C–D. Stamens.—C. Lateral view (×5⅗).—D. Ventral view (5⅗). [After ***Wilbur et al.*** *13485* (DUKE).]

CHIRIQUÍ: Premontane cloud-forest along ridge E of Cerro Horqueta, 1700–1900 m, *Luteyn & Wilbur 4610* (DUKE, F, US), *4621* (DUKE, MICH, MO, NY). Humid forest, top of Cerro Horqueta, 2268 m, *Pittier 3234* (US). S slopes of Cerro Horqueta, N of Boquete, 7200 ft, *Wilbur et al. 13485* (DUKE, MICH, MO). Slopes approaching Cerro Horqueta, 1500–1800 m on trail starting 6.6 km NNE of Boquete, *Wilbur & Luteyn 19249* (DUKE, F, GH, LL, MICH, MO, NY, PMA, US).

2. **Lateropora santafeënsis** Wilbur & Luteyn, Brittonia 29: 261. 1977. TYPE: Panama, *Luteyn & Wilbur 4575* (DUKE, holotype; photo of holotype, NY).

Epiphytic *shrub* 0.5 m tall with stout, glabrous, purplish branchlets and grayish branches. *Leaf blades* coriaceous, elliptic, 3.0–8.5 cm long, 2.0–4.5 cm wide, acutely tapering to both the apex and the base, the margin entire, thickened, slightly revolute, glabrate or with appressed, reddish brown, apparently glandular, strigillose trichomes 0.2–0.3 mm long especially on the lower surfaces, pinnately veined; petioles glabrous, 3–5 mm long, 2.0–3.5 mm in diam. *Inflorescences* axillary, compact, umbelliform racemes 2–3 cm long; peduncle and rachis 8–12 mm long; floral bracts scalelike, ciliate, ovate to suborbicular, somewhat keeled, 2.0–2.2 mm long and about as wide, pedicels stiff, somewhat clavate, glabrous, 5–13 mm long, medially ca. 1 mm in diam., bracteoles 2, subopposite, broadly ovate or suborbicular, ciliate, keeled, appressed, 2.0–2.5 mm long, 1.8–2.2 mm wide, borne on the lower ¼ of the pedicel. *Flowers* with the hypanthium glabrous, campanulate, 3–4 mm high, 4–5 mm in diameter, disarticulating from the pedicel by a marked groove often inconspicuously fringed by glandular trichomes 0.1–0.2 mm long; calyx limb glabrous, 0.5–0.7 mm high, the lobes 5, erect, triangular, acute, 1.5–2.0 mm long, 2.0–2.2 mm wide basally, short ciliate; corolla pale greenish, broadly cylindric to urceolate, 4–5 mm long, medially 5–6 mm in diameter, sparingly and inconspicuously strigillose with trichomes 0.1–0.2 mm long, corolla lobes 5, spreading to weakly reflexed, triangular, acute, 1.5–1.8 mm long, 2 mm wide at base, inside densely tangled villous with white trichomes 0.6–1.0 mm long; stamens 10, the filaments flattened, 2.5–3.0 mm long, broadened basally to ca. 1 mm wide, densely pilose distally; anthers attached near the middle just above the basal bend in the thecae, conspicuously granular, ca. 3 mm long, the tubules vestigial, ca. 0.3 mm long, the thecae with a strongly incurved base ca. 1 mm long or ⅓ the length of the theca, dehiscing by means of a longitudinal slit from the apex to the basal curve.

This species is known only from the holotype.

VERAGUAS: Road beyond Escuela Agrícola Alto Piedra, above Santa Fé and on Pacific Watershed, 800–1000 m, *Luteyn & Wilbur 4575* (DUKE).

10. LYSICLESIA

Lysiclesia A. C. Smith, Contr. U.S. Natl. Herb. 28: 517. 1932. TYPE: *L. caudata* A. C. Smith.

Low, probably epiphytic, *shrubs*. *Leaves* alternate, simple, estipulate, plinerved, subcoriaceous to coriaceous, entire, shortly petiolate. *Inflorescence* axillary or terminal, racemose; floral bracts solitary at the base of the pedicel, minute, triangular; pedicels bibracteolate near the base. *Flowers* with the

hypanthium articulate with the pedicel, the tube 3-winged, the limb erect, 3-lobed, the lobes 3, erect, membranaceous, greatly enlarged; corolla tubular, membranaceous when dry, the lobes (4–)5, triangular, subacute; stamens 8 or 10, alternately unequal, about ⅓ the length of the corolla, the filaments distinct or slightly coherent at the base, alternately unequal, anthers basifixed, equal or alternately slightly unequal, the thecae smooth, submembranous, the tubules about the same width as the thecae but shorter, dehiscent by terminal or slightly oblique pores; style filiform, glabrous or distally pilose, the stigma truncate, the ovary inferior. *Fruit* unknown, but presumably a berry.

Lysiclesia may be recognized by the three large calyx lobes and short, alternately unequal stamens with poroid dehiscence. In this last character, *Lysiclesia* resembles *Orthaea* to which it is seemingly most closely related.

Lysiclesia is a neotropical genus with three closely related species, two in Colombia and one in Panama. Each species is known only from its type collection, and therefore, little is known about the variation within the genus.

Literature:

Luteyn, J. L. and R. L. Wilbur. 1977. New genera and species of Ericaceae (Vaccinieae) from Costa Rica and Panama. Brittonia 29: 255–276.

Smith, A. C. 1932. The American species of Thibaudieae. Contr. U.S. Natl. Herb. 28: 311–547.

1. **Lysiclesia panamensis** Luteyn & Wilbur, Brittonia 29: 261. 1977. TYPE: Panama, *Mori & Kallunki 3602* (MO, holotype; DUKE, isotype; photo, NY). —FIG. 10.

Lax *shrub*, almost vinelike; branches terete to bluntly angled, smooth, short pilose, glabrescent, glaucous, reddish brown when dry. *Leaves* ovate elliptic, (2.5–)3.0–3.5 cm long, (1.2–)1.5–2.0 cm wide, basally obtuse or rounded, abruptly short acuminate, apiculate, glabrous, obscurely 3(–5)-plinerved, midrib nearly plane above but raised beneath, the lateral nerves and the veinlets slightly raised and prominent above, obscure beneath. *Petioles* subterete, flattened adaxially, rugose, short pilose, 2.5–3.0 mm long, 1 mm in diameter. *Inflorescence* axillary, racemose, 2–3-flowered; rachis short pilose, bluntly angled, 1.5–2.2 cm long, ca. 1 mm in diameter, with scattered capitate, glandular trichomes ca. 1 mm long; floral bracts lanceolate, 1.5 mm long, ciliate; pedicels subterete, short pilose, 15–17 mm long, ca. 1 mm in diameter, with scattered, capitate, glandular trichomes; bracteoles ovate lanceolate, acuminate, 3–4 mm long, ca. 1.5 mm wide, strongly nerved, ciliate and bearing capitate, glandular trichomes. *Flowers* with the calyx short pilose, 36–37 mm long, reddish brown, the tube obscured by wings which extend slightly below the base, ca. 4.5 mm long, the limb short campanulate, ca. 2 mm long, 3-parted, the lobes triangular, acuminate, basally ca. 10 mm wide, the margins and the lamina with scattered capitate, glandular trichomes; corolla pink, cylindric but narrowing at the throat, the lobes flaring, membranaceous, short pilose outside except at the very base, in-

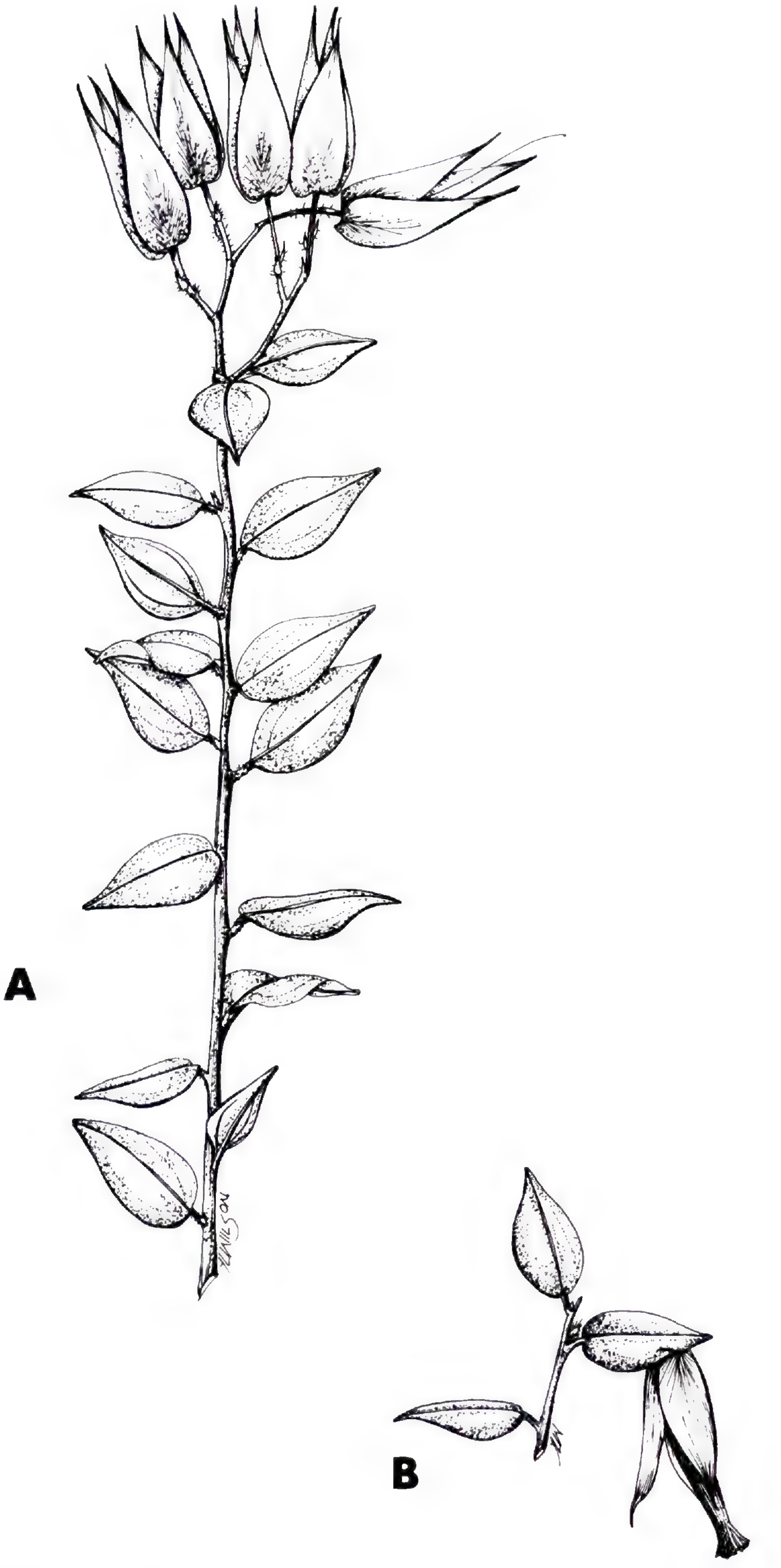


FIGURE 10. *Lysiclesia panamensis* Luteyn & Wilbur.—A. Habit (×7/10).—B. Flower (×7/10). [After *Mori & Kallunki 3602* (MO).]

side and at the throat, ca. 35 mm long, the lobes triangular, obtuse, ca. 1 mm long; stamens alternately ca. 10 mm and 12 mm long, the filaments pilose distally, alternately ca. 5 mm and 8.5 mm long, the anthers including tubules slightly unequal, alternately ca. 5 mm and 5.5 mm long, the thecae 2.5–3.0 mm long, the tubules with terminal or, in shorter stamens, slightly oblique pores; style pilose distally, ca. 36 mm long. *Berry* not seen.

This species is known only from a single collection made on Cerro Jefe in Panama province.

PANAMÁ: Cerro Jefe, cloud forest dominated by *Clusia* and *Colpothrinax cookii*, along trail running NE of summit, 1000 m, *Mori & Kallunki 3602* (DUKE, MO).

11. MACLEANIA

Macleania Hook., Icon. Pl. 2: *pl. 109.* 1837. TYPE: *M. floribunda* Hook.

Tyria Klotzsch, Linnaea 24: 21. 1851. TYPE: *T. salapa* (Benth.) Kl. (= *Ceratostema salapa* Benth.)

Straggly to compact, epiphytic or terrestrial *shrubs*. *Leaves* alternate, petiolate, coriaceous, pinnately veined or plinerved. *Inflorescence* axillary or terminal, subfasciculate or racemose with few to many flowers on deciduously bibracteolate pedicels. *Flowers* with the hypanthium articulate with the pedicel, short cylindric or campanulate; calyx limb erect and spreading (3–4)5-lobed, the segments subacute and triangular; corolla subcylindric or elongate urceolate, 5-parted, the lobes triangular and subacute; stamens usually 10, equal, usually about half as long as the corolla, the filaments distinct or connate, dorsally attached to the anthers near their bases, the anthers stout with strongly granular thecae, the tubules about as long as the anther sacs, either laterally connate or fused into a single tubule, rarely completely distinct, opening by elongate, distinct or fused, introrse clefts; style filiform and about as long as the corolla or longer, basally surrounded by an annular or cupuliform disc; the ovary inferior. *Fruit* a berry with numerous, small seeds.

The genus *Macleania* contains approximately 40 species which range from southern Mexico south along the mountainous highlands into Peru.

Literature:

Smith, A. C. 1932. The American species of Thibaudieae. Contr. U.S. Natl. Herb. 28: 311–547.

Yeo, P. F. 1967. Notes on some species of *Macleania* (Ericaceae). Baileya 15: 45–59.

a. Both anther sacs dehiscing into a single common tubule; filaments distinct or connate.
  b. Filaments distinct; venation plinerved ..... 1. *M. epiphytica*
  bb. Filaments connate for most of their length; venation either plinerved or pinnatinerved.
    c. Calyx wings not extending distally beyond the calyx lobes; venation plinerved; bracteoles borne basally on the pedicel ..... 2. *M. insignis*
    cc. Calyx wings extending distally beyond the calyx lobes and forming per-

pendicular spurlike appendages; venation pinnatinerved; bracteoles borne medially or more distally on the pedicel ..... 3. *M. pentaptera*

aa. Each anther sac dehiscing into its own tubule, the tubules usually longitudinally connate; filaments distinct ..... 4. *M. rupestris*

1. **Macleania epiphytica** A. C. Smith, Ann. Missouri Bot. Gard. 28: 439. 1941. TYPE: Panama: *Allen 2171* (A, holotype).

Epiphytic *shrub* 0.5–1 m tall, vegetatively glabrous throughout; branchlets terete. *Leaf blades* drying coriaceous, oblong elliptic to ovate, 5–8(–10.5) cm long, 2–3(–5) cm wide, basally rounded or broadly obtuse, apically acute to rounded, entire and with a thickened ridgelike border, 5-plinerved, the veins almost plane to moderately prominent above and slightly elevated beneath, the midvein prominently elevated beneath, the veinlets inconspicuous; petioles thick, drying corrugated, 4–8 mm long. *Inflorescences* axillary, usually in the axils of the upper leaves, fasciculate or obscurely racemose, 2–4-flowered; pedicels stout, 5–11 mm long, bracts minute, triangular to deltoid, 0.5–1.0 mm long, bracteoles 2, papery, ovate to deltoid, acute, 0.6–1.2 mm long borne at or a little above the middle. *Flowers* with the hypanthium articulate with the pedicel, prismatic to cylindric at anthesis, 3–5 mm long and distinctly 5-angled, glabrous; calyx limb suberect and about 2 mm high including the lobes, the lobes 0.5–1 mm long, triangular to broadly deltoid with acute to rounded sinuses; corolla tube thinly fleshy, cylindrical at anthesis, glabrous, 17–18 mm long, basally 3–5 mm in diameter, slightly contracted apically, bright red to scarlet, the lobes 5, deltoid to narrowly oblong, acute, 1.5–3 mm long, dark green, internally whitish puberulent; stamens 10, the filaments membranaceous, ca. 3 mm long, distinct, the sacs 4–4.5 mm long with a single rigid tubule ca. 3 mm long opening by an oval cleft 2.5 mm long; style about as long as the corolla.

This species is known only from the mountains of central Panama.

There is now reasonable question as to the distinction of *M. epiphytica* from *M. insignis*. The primary basis for separating the two species has rested upon the separate filaments of *M. epiphytica* in contrast to the connate filaments of *M. insignis*. However populations and specimens have been encountered in Panama with connate, weakly coherent, and separate filaments. Dark green corolla lobes are often noted as occurring on the specimens with separate filaments but this has not been noted on the more northern specimens of *M. insignis* with connate filaments. It is urged that careful notes be made of the flower colors exhibited by these plants.

COCLÉ: Hills N of El Valle de Antón, 1000 m, *Allen 2171* (A). Trail beyond La Mesa towards Los Llanos, N of El Valle de Antón, 800–860 m, *Luteyn 3166, 3173a, 4095* (all DUKE). COLÓN: Río Guanche, *D'Arcy 9712* (MO). Along road into Santa Rita, E of Agua Clara rain gauge, *Kennedy 2742* (MO). Rain forest, Santa Rita Ridge, 5.5–6 mi E of Transisthmian Highway, *Lewis et al. 5376* (MO). Santa Rita Ridge Road, 14 km from Boyd-Roosevelt Highway, *Mori & Kallunki 4920* (MO). PANAMÁ: Primary forest along road from El Llano to Cartí-Tupile, 12 mi from Panamerican Highway, 200–500 m, *Croat 22904* (MO). Cerro Campana, 3000 ft, *Duke 10726(3)* (MO). 19 km above Panamerican Highway, on road from El Llano to Cartí-Tupile, 200–500 m, *Kennedy 2551* (MO). Cloud forest, Cerro Campana, 2600–2800 ft, *Lewis et al. 1941* (MO). Primary forest along El Llano-Cartí-Tupile road, 12 mi above Panamerican Highway, 200–500 m, *Liesner 1219* (DUKE, MO). Road to Cerro

Campana just below Villa Las Minas, 800–900 m, *Luteyn 3186* (DUKE, MO). Cerro Jefe, 3000 ft, *Luteyn & Kennedy 3964* (DUKE). Cerro Campana cloud forest, 850 m, *Luteyn 3978* (DUKE). El Llano-Cartí-Tupile Road, 10–12 km N of Interamerican Highway, 500 m, *Luteyn & Wilbur 4665* (DUKE). VERAGUAS: NW of Santa Fé, 4.2 km from Escuela Agrícola Alto de Piedra, *Mori & Kallunki 4825* (MO). Road beyond Escuela Agrícola Alto Piedra above Santa Fé, Pacific watershed, 800–1000 m, *Luteyn & Wilbur 4565* (DUKE, NY).

2. **Macleania insignis** Mart. & Gal., Bull. Acad. Roy. Sci. Bruxelles 9: 531. 1842. TYPE: Mexico: Veracruz, *Galeotti 1827* (BR, holotype, not seen; W, isotype, not seen; photo, GH, US).

Thibaudia laurifolia Mart. & Gal., Bull. Acad. Roy. Sci. Bruxelles 9: 530. 1842. TYPE: Mexico; Oaxaca, *Galleotti 1814* (BR, holotype not seen; W, isotype not seen; photo, GH, US).

Macleania ovata Klotzsch, Linnaea 24: 20. 1851. TYPE: "in America centrali prope Veraguam," *Warszewicz* (B, holotype, not seen; photo, F).

Macleania cordata var. *linearifolia* Donnell Smith, Bot. Gaz. (Crawfordsville) 16: 12. 1891. TYPE: Guatemala: Pasamala, *Tuerckheim 1332* (US, holotype; photo, NY).

Macleania linearifolia (Donnell Smith) A. C. Smith, Contr. U.S. Natl. Herb. 28: 368. 1932.

Macleania compacta A. C. Smith, Contr. U.S. Natl. Herb. 28: 369. 1932. TYPE: Mexico; Veracruz; near Jalapa, *Pringle 7870* (GH, holotype).

Macleania insignis var. *linearifolia* (Donnell Smith) Standley & L. Wms., Fieldiana, Bot. 31: 172. 1965.

Shrubs often epiphytic 0.5–2(–4) m tall; branchlets terete, light to dark brown; bark peeling, puberulous; young twigs glabrous to puberulous. *Leaf blades* ovate to lance ovate or rarely lance oblong to oblong, (2–)3–8(–12) cm long, (1–)1.5–4 cm wide, basally subcordate, rarely rounded, apically obtuse to acute, entire and slightly revolute, glabrous on both surfaces; 3–5(–7)-plinerved with the secondary nerves originating near the base, ascending, the midvein slightly impressed above and elevated beneath; petioles subterete, rugose, glabrous or rarely puberulous, (1–)2–4 mm long. *Inflorescence* axillary, subfasciculate, (1–)2–3-flowered, basally circumscribed by a few, minute, ovate, ciliate bracts 1.5–2 mm long; pedicels rugose, glabrous or rarely puberulous, (4–)8–16 mm long, bracteoles basal, minutely ciliate, triangular, 1–2 mm long. *Flowers* with the hypanthium glabrous or minutely to moderately appressed short pubescent, prismatic, 3–5 mm long, 3–4 mm in diameter, broadly winged from the base to the sinuses, the wings 0.3–0.5 mm wide; calyx limb ascendent to erect, 1.0–1.5 mm long, the lobes 5, apiculate, narrowly triangular to deltoid, (0.4–)0.8–2.0 mm long, the sinuses either flat or acute, more or less contiguous; corolla elongate urceolate or prismatic, (14–)20–25 mm long, 4–5 mm in diameter, contracted at the throat, externally glabrous to slightly puberulous especially distally, distally sparsely to densely villous internally, the lobes acute, spreading, 1.5–3.0 mm long; stamens 10, 8–12 mm long, the filaments dark brown, glabrous, connate 3–5(–7) mm long, the anther sacs 4.0–5.5 mm long, the single, cylindric-conical tubule 2–3 mm long opening by a broad introrse cleft more than ½ as long as the tubule; style exerted, the stigma peltate.

As interpreted in this account, *Macleania insignis* ranges from the mountains of southern Mexico southward into Panama.

The present treatment is a drastic reduction from the number of species recognized in Smith's (1932) monograph of the genus. The representatives of

this genus with connate filaments in southern Central America have been referred to *M. ovata* Klotzsch. *Macleania ovata* has been generally differentiated from the more northern *M. insignis* by its longer and broader, deltoid calycine lobes which form acute basal sinuses with the adjacent lobes. *Macleania insignis* supposedly had minute calycine lobes less than 1.5 mm long forming a broad, flat sinus between adjacent lobes. There is much greater variability in calycine lobes than was apparent in the relatively few specimens available to Smith, and there is an apparent continuum between the extremes. Hence, there is no way to recognize two taxa based on calycine lobes. Yeo (1967) suggested that *M. ovata* might be best regarded as a geographical subspecies of *M. insignis* but he did not make the combination. The calycine variation does not suggest geographical subspecies since apiculate-lobed plants are found at least as far south as Costa Rica and deltoid, larger lobed plants are to be found in southern Mexico along with the apiculate-lobed plants.

PANAMÁ: Moist upper regions of Cerro Campana, 1000 m, *Allen 2406* (A).

3. **Macleania pentaptera** Hoerold, Bot. Jahrb. Syst. 42: 299. 1909. TYPE: Ecuador; *Sodiro 92/2* (B, not seen; photo, NY).

Epiphytic *shrub*; branchlets terete, glabrous or occasionally sparsely puberulous when young, brownish; root often swollen, tuberous. *Leaf blades* coriaceous, ovate, 8–12 cm long, 4–7 cm wide, glabrous to moderately puberulent beneath, basally strongly cordate or sometimes even amplexicaul, apically rounded or obtuse, rarely subacute, occasionally slightly revolute, pinnately veined, the secondary veins 3 or 4 on each side, arcuately ascending and usually originating near the base; midvein slightly impressed above and prominently elevated beneath, the veins forming a conspicuous reticulum on both sides; petioles thickened, ca. 3 mm long, glabrous or puberulent, rugose. *Inflorescences* axillary, shortly racemose, 3–8-flowered; rachis 0.5–1(–4) cm long; pedicels 12–18 mm long, rugose, glabrous to minutely puberulous; bracts basal, 1–2 mm long; bracteoles 2, medial to supramedial, deciduous, ciliate, deltoid to ovate, 0.5–1 mm long. *Flowers* with the hypanthium obscurely articulate with the pedicel, obconical, glabrous or minutely puberulous distally, 10–13 mm long, 5-winged to the sinuses, the wings fleshy, ca. 0.5 mm broad, projecting above the rim of the calyx to form a coriaceous spur 1–4 mm long; calyx limb dilated, the lobes apiculate, 0.2–0.6 mm long; corolla scarlet to orange red, green distally, cylindric, 13–20 mm long, ca. 5 mm in diameter at thickest point, slightly contracted below the throat, externally glabrous, internally densely pilose distally with trichomes ca. 0.5 mm long, the lobes erect, triangular, acute, ca. 3 mm long, basally 1.5 mm wide, frequently bearing a perpendicular, fleshy, oblong spur; stamens 10, 7–8.5 mm long, about ½ as long as the corolla, the filaments connate, glabrous, 2–3 mm long, the anther sacs 5–7.5 mm long terminated by a single, elongate, conical tubule 3–5.5 mm long opening by an introrse cleft about ½ its length; stigma truncate, the style often slightly exserted from the corolla tube.

The range of this species has only recently been extended to include eastern Panama; it is otherwise known only from Colombia and Ecuador.

DARIÉN: Cloud forest, Cuasí-Caña Trail between Cerro Campamiento and La Escalera to "Paramo," E of Tres Bocas, *Kirkbride & Duke 1303* (MO). Tres Bocas on the Río Cuasí, *Kirkbride & Duke 1378* (MO), *1379* (MO, NY).

4. **Macleania rupestris** (H.B.K.) A. C. Smith, Phytologia 1: 131. 1935.—FIG. 11.

Thibaudia rupestris H.B.K., Nov. Gen. Sp. Pl. 3: 270. 1818. TYPE: Colombia; near Loxa and Alto de Pulla, *Humboldt & Bonpland* (P, holotype, not seen; photo, NY).
Psammisia rupestris (H.B.K.) Klotzsch, Linnaea 24: 45. 1851.
P. alpicola Klotzsch, Linnaea 24: 45. 1851. TYPE: Colombia, *Moritz 1349* (B, holotype, not seen; photo, NY).
P. glabra Klotzsch, Linnaea 24: 46. 1851. TYPE: "in alpibus Veraguae Americae centralis," *Warszewicz* (B, holotype, not seen; photo, F, GH, NY, US).
P. costaricensis Klotzsch, Linnaea 24: 47. 1851. TYPE: "in Americae centralis montibus," *Warszewicz* (B, holotype, not seen; photo, GH, US).
Macleania turrialbana Donn. Sm., Bot. Gaz. (Crawfordsville) 27: 339. 1899. TYPE: Costa Rica: Cartago; Volcán Turrialba, *Pittier 7546* (US, holotype; F, GH, isotypes; photo of holotype, NY).
M. costaricensis (Klotzsch) Hoerold, Bot. Jahrb. Syst. 42: 268. 1909.
M. glabra (Klotzsch) Hoerold, Bot. Jahrb. Syst. 42: 268. 1909.
M. alpicola (Klotzsch) Hoerold, Bot. Jahrb. Syst. 42: 269. 1909.
M. sodiroi Hoerold, Bot. Jahrb. Syst. 42: 302. 1909. TYPE: Ecuador.
M. trianae Hoerold, Bot. Jahrb. Syst. 42: 303. 1909. TYPE: Colombia.
M. irazuensis Blake, Proc. Biol. Soc. Wash. 35: 121. 1922. TYPE: Costa Rica; Cartago, Volcán Irazú, *Popenoe 1017* (US, holotype).
M. racemosa Cuf., Arch. Bot. Sist. 9: 199. 1933. TYPE: Costa Rica; Volcán Poás, *Cufodontis 717* (W, holotype, not seen, photo F, GH; F, isotype).

Epiphytic or terrestrial *shrub* 0.6–2.0 m high; branchlets subterete, glabrous to rarely moderately puberulent. *Leaf blades* oblong to ovate oblong, rarely elliptic, (2–)4–8(–13.5) cm long, (1.2–)2–5(–7.5) cm wide, basally cuneate to broadly rounded, apically broadly rounded to acute, marginally subentire and slightly revolute, usually glabrous both above and below but occasionally puberulent or spreading short pubescent on the lower surface near the base, occasionally sparsely punctate above; pinnately veined, the midvein slightly impressed above and prominently elevated beneath, the 2–4, arcuate-ascending, secondary veins on each side plane above and prominently elevated beneath, reticulate veinlets also flush above and slightly elevated beneath; petioles rugose, usually glabrous, 4–10 mm long, narrowly winged above. *Inflorescences* axillary near the ends of the branches, racemose, 4–20-flowered, glabrous throughout or occasionally moderately spreading short pubescent; rachis striate, 1–8 cm long; pedicels striate, glabrous to puberulous, reddish, (7–)10–24 mm long; bract single, deltoid or ovate to oblong, often ciliate, 2–5(–7) mm long; bracteoles 2, broadly deltoid to oblong, 1–2(–3) mm long. *Flowers* with the hypanthium short cylindric, ca. 2.5 mm long, 4 mm in diameter, deep maroon; calyx limb flaring, 2–5 mm long including the lobes, the lobes 5, apiculate, ca. 1 mm long; corolla (12–)18–22 mm long, 6 mm in diameter, cylindric urceolate, deep red or pinkish red, the tube contracting at the throat to ca. 3 mm in diameter, the lobes deltoid to oblong, acute, 1.5–2.5 mm long, pale red, pink to white, ciliate; stamens 10, 9–14 mm long, the filaments distinct, glabrous or marginally short pilose distally, 2–4 mm long; the anther sacs basally and apically incurved, 4–7 mm long, the tubules laterally connate throughout, rarely distinct nearly to the

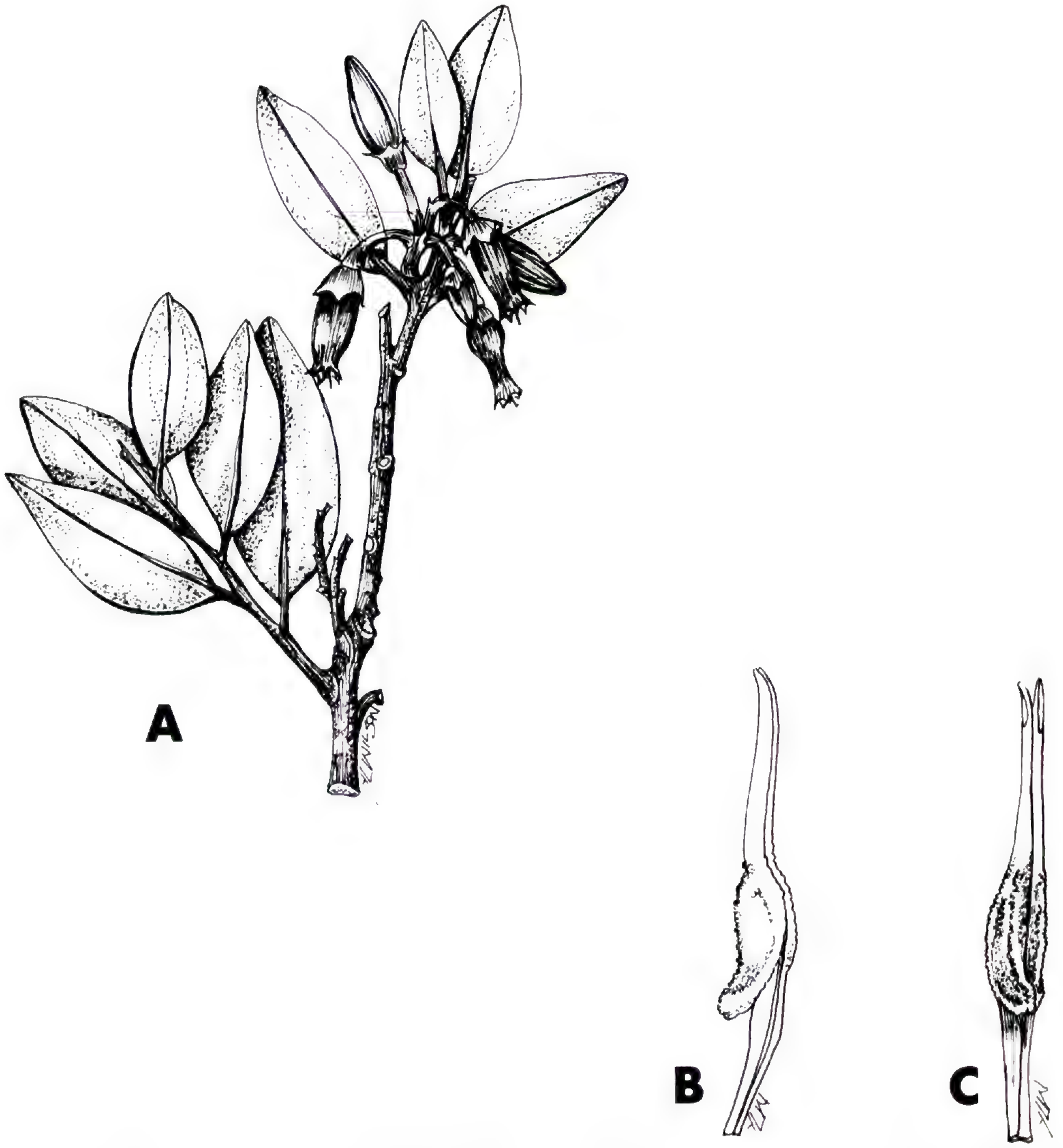


FIGURE 11. *Macleania rupestris* (H.B.K.) A. C. Smith.—A. Habit (×1).—B–C. Stamens. —B. Lateral view (×5⅖).—C. Ventral view (×5⅖). [After *Wilbur & Teeri 13077* (DUKE).]

base, rigidly and narrowly cylindric conical, 3.5–6 mm long, opening by elongate, introrse clefts about ⅓–½ the length of the tubule; stigma truncate, the style glabrous. *Berry* dark bluish black.

As interpreted here *Macleania rupestris* occurs in western Nicaragua, Costa Rica and western Panama and from Venezuela and Colombia southward into Peru.

A.C. Smith (1932: p. 378) in his revision of the genus *Macleania* noted a slight morphological distinction which separates the Central American *M. glabra* from the South American *M. nitida* in the sense of Hoerld (= *M. rupestris* (H.B.K.) A.C. Sm.). His key reads as follows.

Tubules slightly shorter than the anther sacs, rarely subequal (South America) ..... *M. rupestris*
Tubules slightly longer than the anther sacs, rarely subequal (Central America) ..... *M. glabra*

A survey of many specimens from both South and Central America failed to demonstrate any distinction in the ratios of tubules to anther sac between Central and South American specimens. Almost all specimens examined from Costa Rica and Panama had anther sacs longer than the tubules which is contrary to the key. The ample material accumulated in the past forty-five years confirms Smith's suspicion that combining the two supposed taxa is the best course to be followed since no other consistent differences have been detected.

CHIRIQUÍ: Cerro Punta, 2000 m, *Allen 1562* (MO, NY). Summit and SW face of Cerro Copete, 9000 ft, *Allen 4901* (MO, US). Slopes of Las Cumbres near Cerro Punta, *Croat 13702* (DUKE, MO). Wooded slopes on Cerro Horqueta, 1650 m, *Croat 26952* (MO). 10 mi above Boquete on road to Volcán Barú, 2600 m, *Croat 34826* (MO). Eastern slope of Volcán Barú, 8 mi from Boquete, 2300–2400 m, *Croat 34996* (MO). Alto Respinga and above, 2800 m, *D'Arcy 9951* (MO). Potrero Muleto to summit of El Barú, *D'Arcy 10163* (DUKE, MO). Oak forest at 2400 m on E slope of Volcán de Chiriquí, *Davidse & D'Arcy 10217* (DUKE, MO, NY). Elfin forest on ridges above Potrero Muleto on Volcán de Chiriquí, 3000 m, *Davidse & D'Arcy 10258* (DUKE, MO, NY). Bajo Chorro, 6000 ft, *Davidson 158* (A, F, MO, US); *Davidson 609* (F). Volcán de Chiriquí, 9000 ft, *Davidson 975* (A, F, MO). Peak of Volcán de Chiriquí, 11900 ft, *Davidson 1315* (MO). Cerro Respinga on Boquete Trail, 2000–2500 m, *Gentry 5930, 5947* (both DUKE, MO). La Peña Blanca cloud forest, 5500 ft, *Hagen 2001* (A, NY). Cerro Horqueta, 5800 ft, *Lewis et al. 550* (MO). Upland pastures 2–2.5 km E of Cerro Punta, 7150–7200 ft, *Luteyn 3047* (DUKE, F, MO). Premontane cloud forest along ridge E of Cerro Horqueta, 1700–1900 m, *Luteyn & Wilbur 4592* (DUKE). Above timberline on W side of Volcán Barú, 3000 m, *Mori & Bolton 7343* (MO). Oak forest 2.5 km SE of Cerro Punta, *Mori & Kallunki 5675* (MO). Bajo Grande, 1–3 km E of Cerro Punta, 2000–2200 m, *Nee 10027* (DUKE, MO). Volcán Chiriquí, 3000–3371 m, *Pittier 3102* (US). Near peak Volcán de Chiriquí, 11900 ft, *Terry 1315* (A, F). Boquete, El Velo, 6150 ft, *Stern et al. 2001* (US). Boquete, Finca Collins, 5800–6700 ft, *Stern et al. 2024* (US). W slope of El Barú, 6000–7000 ft, *Tyson & Loftin 5948* (DUKE, FSU, MO); *Tyson & Loftin 5958* (DUKE, FSU). W slope of El Barú, 8000–9000 ft, *Tyson & Loftin 6127* (DUKE, FSU). W slope of El Barú, 1000–1100 ft, *Tyson & Loftin 6147* (DUKE, FSU). 5 mi NE El Volcán, 7000 ft, *Tyson 6344* (DUKE). Cerro Punta, 6000 ft, *Tyson 7026* (DUKE). Halfway between Cerro Punta and Bambito, 5600 ft, *Wilbur et al. 10891* (DUKE). W slope of Volcán de Chiriquí, 8600 ft, *Wilbur 11030* (DUKE, MO). Trail between Cerro Punta and Quebrado Bajo Grande, 2000–2100 m, *Wilbur et al. 11896* (DUKE). Steeply cut bank above trail between Bajo Quiel and Bajo Mono 6 mi NW of Boquete, 1450 m, *Wilbur et al. 12015* (DUKE). Trail along Quebrado Grande to top of Paso de Respingo on trail to Boquete, 2100–2400 m, *Wilbur et al. 15117* (DUKE, F, MICH, MO); *Wilbur et al. 15134* (DUKE). Old lava field 4 mi NW of El Hato del Volcán near Río Macho de Monte, 1800 m, *Wilbur & Teeri 13077* (DUKE, MO). Mossy forest E of Guadeloupe along Río Chiriquí Viejo 2 mi NE of Cerro Punta, *Wilbur & Teeri 13101* (DUKE, MO). Quebrado Bajo Grande 2 mi E of Cerro Punta, 6900 ft, *Wilbur & Teeri 13138* (DUKE, MO). Casita Alta, Volcán de Chiriquí, 1500–2000 m, *Woodson et al. 817* (MO, NY); *Woodson et al. 976* (A, MO, NY). Loma Larga to summit, Volcán de Chiriquí, 2500–3380 m, *Woodson et al. 1070* (A, MO, NY). Casita Alta to Cerro Copete, 2300–3300 m, *Woodson & Schery 356* (MO). Potrero Muleto to summit, Volcán de Chiriquí, 3500–4000 m, *Woodson & Schery 381* (MO, NY).

12. MONOTROPA

Monotropa L., Sp. Pl. 1: 387. 1753; Gen. Pl. ed. 5. 183. 1754. LECTOTYPE: *M. uniflora* L.

Hypopitys Hill, Brit. Herb. 221. 1756.
Hypopithys Scopoli, Fl. Carniolica 1: 285. 1771. TYPE: *H. multiflora* Scop.

Fleshy *herbs* lacking chlorophyll, blackening in drying; tawny, reddish or orangey to translucently white; mycorrhizal root parasites (often considered saprophytic); flowering stems nodding at tip but erect in fruit, 1–15 flowers

each borne in the axil of an upper more or less appressed, erose-margined bract, the pedicels recurved, ebracteolate. *Flowers* (3–)4–5(–6)-parted; calyx of 1–5, lanceolate, deciduous, bractlike scales; corolla campanulate, (3–5)6-parted, the petals erect, imbricate, scalelike, distinct, basally saccate and tardily deciduous; stamens 8–10(–12), the filaments distinct, terete, subulate, pubescent, the outer whorl (opposite the petals) shorter than the inner, the anthers short, kidney-shaped, 1-locular at anthesis, opening by a single terminal slit or by ends of a slit which may later open along its entire length; pollen grains single; nectaries of 8–10 paired lobes between the filament bases; stigma funnel-shaped to discoid, obscurely 4–6-lobed, the style columnar, thick, fleshy, the ovary superior, (8)10-lobed, (4–)5(–6) loculate basally with axile placentation, 1-locular above with 4–5, bilobed parietal placentas. *Capsule* globose to ovoid, 8–10-grooved, erect, loculicidally 4–6-valved; seeds numerous, minute, tailed.

Monotropa is a genus of perhaps only two circumpolar species, *M. uniflora* L. and *M. hypopithys* L., both known from Central America. The genus has usually been regarded as a saprophyte or less commonly as a parasite but the studies of Björkman (1960) indicate that it is better considered an achlorophyllous mycotrophyte in which the fungal associate is intermediate between *Monotropa* and its ultimate host.

Literature:

Björkman, E. 1960. *Monotropa hypopitys* L.—an epiparasite on tree roots. Physiol. Pl. (Copenhagen) 13: 308–327.

Gupton, O. 1962. An analysis of the taxonomic criteria as applied to the genus *Monotropa*. Unpublished Ph.D. thesis. University of North Carolina, Chapel Hill.

Nowicke, J. W. 1966. Pollen morphology and classification of the Pyrolaceae and Monotropaceae. Ann. Missouri Bot. Gard. 53: 213–219.

Wallace, G. B. 1975. Studies of the Monotropoideae (Ericaceae): taxonomy and distribution. Wasmann J. Biol. 33: 1–88.

1. **Monotropa uniflora** L., Sp. Pl. 1: 387. 1753. TYPE: Virginia, *Clayton 245* (LINN, holotype, not seen).—FIG. 12.

Hypopitys uniflora (L.) Crantz, Inst. Rei Herb. 2: 476. 1766.
Monotropa morisoniana Michx., Fl. Bor. Amer. 1: 266. 1803. TYPE: Carolina, *Michaux* (P, not seen).
M. morisoni Pers., Syn. Pl. 1: 469. 1805.
M. coccinea Zucc., Flora 15: 100. 1832. TYPE: Mexico, *Karwinski* (M, holotype, not seen).
M. coccinea var. *mexicana* Lange, Vidensk. Meddel. Naturhist. Dansk. Foren. Kjøbenhavn 7: 119. 1866.
M. coccinea var. *nicaraguensis* Lange, Vidensk. Meddel. Naturhist. Dansk Foren. Kjøbenhavn 7: 119. 1866. Nicaragua, *Oersted s.n.* (C, holotype; not seen).
M. uniflora var. *coccinea* (Zucc.) Domin, Abh. Böhm. Ges. Wiss. 5. 1915.
M. uniflora var. *australis* (H. Andres ex Domin) Domin, Abh. Böhm. Ges. Wiss. 6. 1915.
M. brittonii Small, J. New York Bot. Gard. 28: 7. 1927. TYPE: Florida; Palm Beach Co., *Small et al. 9219* (NY, lectotype).
M. uniflora f. *rosea* Fosberg, Castanea 20: 59. 1955. TYPE: Virginia, Limberlost, Shenandoah National Park, *Fosberg 36143* (US, holotype).

FIGURE 12. *Monotropa uniflora* L. Habit (×1). [After *Mowbray* 7.2.63 (DUKE), North Carolina.]

Glabrous, scapose *herbs*, arising from perennial root masses. *Scapes* (5–)13–30 cm tall, 2–5 mm in diameter, terete, somewhat fleshy, striate, bracteate. *Leaves* (bracts) congested both basally and distally, oblong to lanceolate, 6–16(–20) mm long, (2–)3–5(–10) mm wide, apically acute, basally rounded and sessile, the margins entire or somewhat erose. *Flowers* solitary, nodding at anthesis, erect in fruit, perianth 5-merous; sepals 13–16 mm long, 3–7 mm wide, lanceolate, apically obtuse or acute, the margins erose; petals 5–8, 8–16(–20) mm long, (4–)5–15 mm wide, basally saccate, oblong, obovate or spatulate, apically rounded, the margins becoming erose distally; stamens (8–)10(–14), alternately slightly unequal (ca. 1 mm difference in length), the filaments terete, 11–12 mm long, the anthers reniform, appearing peltate, ca. 2 mm in diameter; stigma funnel-shaped, obscurely 5-lobed, 2–6 mm in diameter, the style short, thick, 2–7 mm long, 2–3(–5) mm in diameter; ovary 5–6-locular, globose or ovoid, ca. 7 mm long, 6 mm in diameter. *Capsule* ca. 11 mm long; seeds 1 mm long, spindle-shaped.

Monotropa uniflora is an often clump-forming herb, white to rose pink or carmine in color, but drying black. It is found in the deep shade of humid forest floors in Central America, and has been rarely collected. Nowicke (1966) indicated that the minor differences in shape and size of pollen grains between a single specimen from Labrador and one from Guatemala "suggests that they may be distinct." She treated them respectively as *M. uniflora* L. and *M. coccinea* Zucc., but we are following Wallace's (Wasmann J. Biol. 33: 37–42. 1975) treatment which does not consider *coccinea* as distinct. A larger series of specimens should be examined palynologically before acceptance of Nowicke's suggestion. Wallace's map of the distribution of *M. uniflora* shows the species to range widely through eastern North America and across Canada to the Pacific Northwest. It occurs from Japan and Korea across southern China and through the Himalayas. Its range in Latin America is disjunct from that in eastern North America and also within Latin America since it occurs in Mexico, Central America and Colombia.

CHIRIQUÍ: Trail from Paso Ancho to Monte Lirio, upper valley or Río Chiriquí Viejo, 1500–2000 m, *Allen 1500* (MO, NY). El Barú above Boquete, 1200–1800 m, *D'Arcy 9890* (MO). E slopes of Volcán de Chiriquí, WNW of Boquete, oak forest, 2400 m, *Davidse & D'Arcy 10193* (DUKE, MO). Montane forest at lower limit of oaks on steep slope about 9 km by road WNW of Boquete, 1870 m, *Davidse & D'Arcy 10295* (MO).

13. PERNETTYA

Pernettya Gaud., Voy. Freycinet Bot. 454. *tab.* 67. 1826 [1829]. nom. conserv.
TYPE: *P. empetrifolia* (Lam.) Gaud. = *P. pumila* (L.f.) Hook.

Pernettia Gaud., Ann. Sci. Nat. (Paris) ser. I. 5: 102. 1825. TYPE: *P. empetrifolia* (Lam.) Gaud.

Straggly to densely bushy *shrubs* with depressed, sprawling to erect stems. *Leaves* alternate, persistent, coriaceous or membranaceous, denticulate or serrulate, short petiolate. *Inflorescence* with flowers usually solitary in the axils of the upper leaves or rarely in axillary racemes; pedicels bracteate, nodding,

bibracteolate, indistinctly articulated just beneath the calyx. *Flowers* with the calyx persistent with a short tube and 5 lanceolate to elliptic, acute lobes; corolla tube urceolate, cylindric to ovoid or subglobose, white or white tinged with pink or rose, the lobes 5, less than ⅒ as long as the corolla tube, reflexed; stamens 10, included well within the corolla, the filaments slightly dilated below, glabrous, the anthers mostly oblong or oval, dehiscing apically by terminal pores, 2 slender awns terminating each anther sac; stigma punctate, the style slender, cylindric, persistent, the ovary superior, 5-loculate, usually subspheroid. *Berry* subglobose to globose, somewhat fleshy and even succulent; seeds numerous, small, angular, compressed.

This is a montane genus of perhaps 15 species. It ranges from Central Mexico south throughout Central America and western South America to southern Argentina and Chile. It also occurs in New Zealand and Tasmania.

Literature:

Camp, W. H. 1939. Studies in the Ericales. IV. Notes on *Chimaphila, Gaultheria* and *Pernettya* in Mexico and Adjacent Regions. Bull. Torrey Bot. Club 66: 7–28.

Sleumer, Hermann. 1935. Revision der Gattung *Pernettya* Gaud. Notizbl. Bot. Gard. Berlin-Dahlem, 12: 626–655.

1. **Pernettya coriacea** Klotzsch, Linnaea 24: 85. 1851. TYPE: Costa Rica, *Warscewicz* (B, holotype, not seen).—FIG. 13.

P. setigera Klotzsch, Linnaea 24: 85. 1851. TYPE: Costa Rica; "Vulcán Carthago" [Irazú], *Warscewicz* (B, holotype, not seen).

P. ciliaris var. *alpina* Donnell Smith, Bot. Gaz. (Crawfordsville) 25: 148. 1898. TYPE: Costa Rica; Cerro de la Muerte, 3100 m, *Pittier* (Costa Rican herb. no. *10543*) (US, holotype).

Gaultheria alpina (Donnell Smith) Sleumer, Notizblatt Bot. Gart. Berlin-Dahlem 13:207. 1936.

Shrubs erect, bushy, (0.1–)0.2–1.2(–3) m tall; branches moderately to densely short puberulous, moderately or densely strigose or setose on the younger growth but sometimes estrigillose or nonsetose. *Leaves* alternate, persistent, usually with the internodes shorter than the leaves and the leaves strongly overlapping, (6–)12–20(–25) mm long, (3–)5–8(–12) mm wide, coriaceous, narrowly to broadly elliptic or oblong elliptic, glabrous above, beneath glabrous to variably strigillose with short trichomes usually restricted to the midvein but occasionally uniformly dispersed across the surface; margins minutely crenulate serrulate with 6–10 or more teeth on each side, thickened and drying somewhat revolute; petioles mostly 1–4 mm long. Racemes axillary, usually puberulous and often with strigillose trichomes, the bractlets usually several, ovate, oblong to lanceolate, appressed, persistent, 1–3 mm long; pedicels (1–)4–10(–12) mm long. *Flowers* with the calyx persistent, the tube 0.5–1 mm long, the lobes lance ovate to lanceolate, 2–3 mm long, acute, minutely puberulous ciliate and occasionally glandular denticulate, externally often minutely and inconspicuously puberulous especially apically; corolla urceolate, white to lightly roseate tinged, mostly (3.5–)5–7 mm long including the lobes, the lobes erect to reflexed, 0.8–

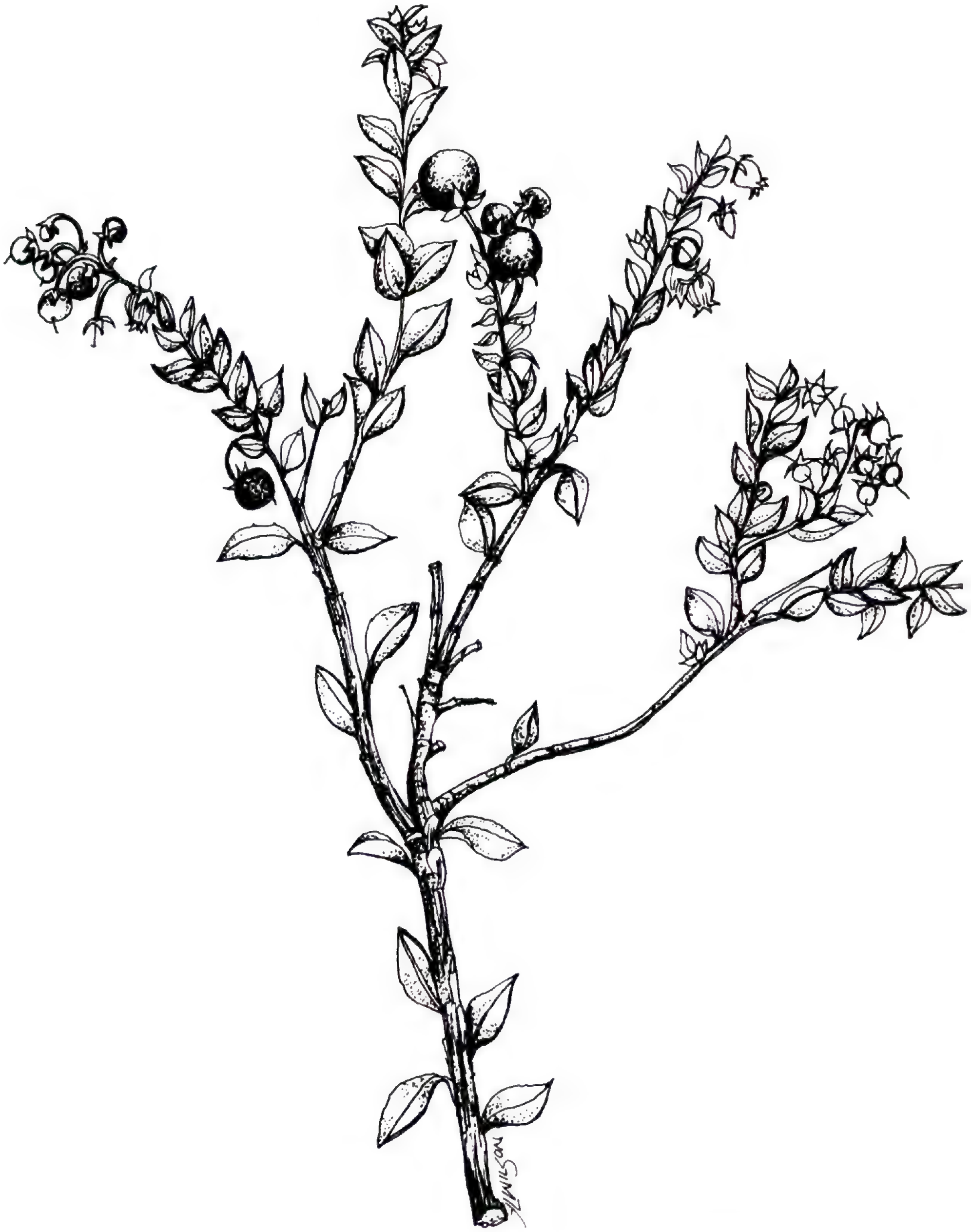


FIGURE 13. *Pernettya coriacea* Klotzsch. Habit (×1). [After *Wilbur & Teeri 13334* (DUKE).]

1.2 mm long, stamens 10, less than ⅔ as long as the corolla, the filaments minutely granular but glabrous, ca. 2 mm long, dilated, ca. 0.5 mm wide basally, ca. 0.1 mm wide above, the anthers oblong, reddish brown, ca. 1 mm long, dehiscing by a terminal cleft, each sac terminated by 2 slender, straight awns ca. 0.3 mm long; stigma ca. 0.3 mm in diameter glabrous, little wider than the persistent,

glabrous style, the style (1.5)2–2.5 mm long, the ovary globose to subglobose, glabrous to densely short pubescent, ca. 1.5 mm in diameter. *Berry* dark blackish purple, 8–10 mm in diameter, glabrous to densely spreading short pubescent; seeds numerous, compressed, angulate, golden, 0.4–0.6 mm long, the surface shallowly and irregularly reticulate with elongate depressions.

The traditional taxonomic treatment of the polymorphic, highly variable complex to which this species belongs recognized at least one species, *P. ciliata* (Schlect. & Cham.) Small, from Mexico and perhaps Guatemala, a second species, *P. coriacea* Klotzsch, from Costa Rica and western Panama, and a third species, the highly variable *P. prostrata* (Cav.) DC., from the South American Andes. This third species is sometimes attributed also to the higher peaks of the Costa Rican Talamancas. Additional taxa have also been proposed: Camp (1939) recognized six species from Mexico; Standley and Williams (1966) accepted two species for Guatemala and thought there might well be a third. Standley (1938) recognized only one species from Costa Rica in spite of Sleumer's (1935) inclusion, the otherwise South American *P. prostrata* var. *purpurea*. Sleumer was able to separate *P. ciliata* from *P. prostrata* in his key only by geography, admitting that the two species can scarcely be differentiated morphologically. Sleumer provided no descriptions to indicate what tendencies he felt differentiated the two supposed species. Within the extensive range of this variable complex there is much variation in such features as habit, leaf shape, pubescence of leaves, stems and ovaries as well as in the shape and dimensions of the flowers. The resolution of this small but knotty problem will depend upon intensive field study throughout the range of the complex; for the moment we revert to the traditional treatment of the Panamanian representatives.

CHIRIQUÍ: Llanos on slopes of Volcán de Chiriquí along Río Chiriquí Viejo, 1200 m, *Allen 1006* (F, GH, MO, NY, US), 1300 m, *Allen 1547* (GH, MO, NY, US). N forested face of Cerro Copete, an E spur of Chiriquí Volcano, 8000–8500 ft, *Allen 4870* (MO, US). Summit and SW face of Cerro Copete, 9000 ft, *Allen 4898* (MO, US). Llano del Volcán, *Allen & Fairchild 3459* (GH, NY, US). Camino a Cerro Punta cerca de 5 kms NW del Hato de Volcán, *Correa 1379* (DUKE, MO). Volcán Barú, 1 mi from Summit on upper E slopes, 3000 m, *Croat 34916* (MO). Summit of El Barú, 3225–3447 m, *Croat 34928* (MO). Lava flow between El Hato and Bambito, *D'Arcy 10042* (DUKE, MO). Peak between Barú and Respinga, ca. 3000 m, *D'Arcy 10094* (DUKE, MO). Potrero Muleto to summit of El Barú, *D'Arcy 10158* (DUKE, MO), *D'Arcy 10172* (MO). 11 km WNW of Boquete, ridges looking down on Potrero Muleto, *Davidse & D'Arcy 10237* (DUKE, MO, NY). Lava flow 3 km NE of El Hato del Volcán at base of Volcán de Chiriquí, 1500–1800 m, *Davidse & D'Arcy 10334* (DUKE, MO, NY). Potrero Muleto, Volcán de Chiriquí, 10400 ft, *Davidson 1012* (A, F, MO). Lava fields near town of Volcán, 4600 ft, *Duke 9221* (MO, US). Llanos between El Hato and Cerro Punta, *Ebinger 794* (MO, US). Lava flow 0.5 mi S of Bambito, *Lazor 2716* (FSU, SCZ). Open grassland on lava fan 3 mi E of El Volcán, 4500 ft, *Little 6072* (F, US). Llanos of lava outside El Hato del Volcán on road to Cerro Punta, 6000 ft, *Luteyn 3052* (DUKE, MO). Summit of Chiriquí Volcano, 3025–3374 m, *Maxon 5348* (NY). W slopes of Volcán de Chiriquí, 1500 m, *Mori & Kallunki 5690* (DUKE, MO). Savanna 1 mi S of Bambito, *Partch 69–25* (MO). Around El Potrero Camp, Chiriquí Volcano, 2800–3000 m, *Pittier 3078* (GH). Llanos del Volcán, 1120–1200 m, *Seibert 322* (A). Peak of Volcán de Chiriquí, 11500 ft, *Terry 1296* (F). Peak, Volcán de Chiriquí, 11900 ft, *Terry 1334* (A, F). Windswept canyon, 8 mi NE El Volcán, 8100–8400 ft, *Tyson 835* (FSU, MO). 3 mi N of El Volcán on old lava flow, 5000 ft, *Tyson 5736* (FSU, MO, SCZ). W slope of El Barú, 6000–7000 ft, *Tyson & Loftin 5947* (DUKE, FSU). Top of El Barú above 11000 ft, *Tyson & Loftin 6164, 6165* (both DUKE, FSU); *Tyson & Loftin 6176* (DUKE, FSU). Cerro Pando, valley of the upper Río Chiriquí Viejo, *White 17* (MO). Valley of Río Chiriquí Viejo on

llanos near Bambito, *White 45* (NY). Lava flow NE of El Hato del Volcán near Aguacate, 1800–1900 m, *Wilbur et al. 10972* (DUKE, MO, NY, US). Lava field 5 mi NE of El Hato del Volcán, *Wilbur et al. 11864* (DUKE, NY, US). Lava flow between Volcán de Chiriquí and Cerro Aguacate, 6500–7200 ft, *Wilbur & Teeri 13334* (DUKE). Four m NE of El Hato del Volcán, 1950 m, *Wilbur et al. 15415* (DUKE). Lava field 3 km S of Bambito and 4.2 km N of El Hato del Volcán, 1400–1600 m, *Wilbur & Luteyn 19421* (DUKE). Potrero Muleto to summit, Volcán de Chiriquí, 3500–4000 m, *Woodson & Schery 380, 436* (both GH, MO, NY). Loma Larga to summit, Volcán de Chiriquí, 2500–3380 m, *Woodson et al. 1046, 1093* (both A, MO, NA, NY).

14. PSAMMISIA

Psammisia Klotzsch, Linnaea 24: 42. 1851. LECTOTYPE: *P. falcata* (H.B.K.) Kl.

Epiphytic or terrestrial *shrubs*. *Leaves* coriaceous, plinerved or pinnately veined, petiolate. *Inflorescence* axillary or terminal, subfasciculate or racemose with few to many flowers; pedicels deciduous bibracteolate, usually with a sharply delineated disarticulation groove just beneath the flower. *Flower* with the hypanthium short cylindric or campanulate, the limb erect or spreading; calyx lobes (2–4)5, ovate or triangular, apiculate or acute; corolla subcylindric, elongate urceolate or subglobose, 5-lobed, the lobes triangular and subacute; stamens(8)10(12), equal, often nearly as long as the corolla, the filaments distinct or connate, the anthers inserted dorsally near the base, firm, stout with strongly granular thecae, the tubules distinct, ¼ to about as long as the anther sacs, opening by elongate introrse clefts, the connectives either all laterally and distally 2-spurred or alternately spurred and spurless (rarely spurs obscure or lacking), the spurs either acute and conspicuous or rounded and not very apparent; style filiform and often exserted. *Fruit* a leathery berry.

This genus consists of approximately 55 species ranging from Costa Rica southward into Bolivia and eastward to French Guiana and Trinidad.

a. Leaves pinnately veined.
  b. Leaves 24 cm long or less and 4-times as long as wide or less ..... 2. *P. darienensis*
  bb. Leaves 25 cm long or more and (5–)6-times as long as wide or more ..... 4. *P. panamensis*
aa. Leaves plinerved.
  c. Corolla less than 10 mm long; stamens 4–5 mm long; filaments 1–2.4 mm long, distinct; tubules 1–1.5 mm long; disarticulation groove beneath hypanthium lacking ..... 3. *P. dolichopoda*
  cc. Corolla 20 mm long or longer; stamens 8 mm long or more; filaments 3 mm long or longer, connate or rarely distinct; tubules 2–4.5 mm long; disarticulation groove beneath hypanthium sharply delineated.
    d. Rachis of inflorescence 2 cm or longer; anthers including tubules 5.5 mm long or more; calyx lobes ovate or oblong ovate, apiculate, 1–3 mm long ..... 1. *P. columbiensis*
    dd. Rachis of inflorescence 1 cm long or less; anthers including tubules (5–)7 mm long or less; calyx lobes triangular, acute, ca. 1.5 mm long .. 5. *P. ramiflora*

1. **Psammisia columbiensis** Hoerold, Bot. Jahrb. Syst. 42: 303. 1909. TYPE: Colombia, *Lehmann 4452* (B, holotype, not seen).

Shrub 1–2 m tall, often becoming vinelike with branches scrambling to 7 m; branches terete or subterete, smooth or striate, glabrous or minutely puberulous, reddish or grayish brown when dry. *Leaves* chartaceous or sub-

coriaceous, oblong, elliptic or lance elliptic, 9–14 cm long, 2–4.5 cm broad, basally cuneate and decurrent on the petiole, apically long acuminate, entire, glabrous, 3–5-plinerved, the midrib and the lateral nerves slightly impressed or raised above, conspicuously raised beneath, the veinlets impressed or more frequently raised above, raised and usually conspicuous beneath; petioles 4–6 mm long, 1.5–2 mm in diameter, glabrous, dark reddish brown. *Inflorescence* axillary, racemose, 8–12-flowered; rachis subterete or bluntly angled, glabrous, 2–6 cm long; floral bracts ovate, acute to acuminate, 2–3(–6) mm long, 1–1.5 mm wide, glabrous, marginally scarious; pedicels cylindric, glabrous, 10–20 mm long and 1–1.5 mm in diameter, lengthening to 40; bracteoles 2–3(–4) mm long, similar to the floral bracts. *Flowers* with the hypanthium glabrous, campanulate, slightly rugose, 2–3 mm long, the calyx limb 2–4 mm long including the lobes, the lobes ovate or oblong ovate, apiculate, 1–3 mm long; corolla cylindric, narrowed at the throat, glabrous, 22–27 mm long, 5–7 mm in diameter, the lobes oblong, acute or obtuse, ca. 2–3 mm long; stamens 10, 8–13 mm long, the filaments connate (rarely loosely united in Ecuadorian material) into a distally ciliate tube 3–4 mm long, the connective conspicuously spurred (Panama–Colombia) or seemingly unspurred (Ecuador); the anthers 5.5–11 mm long including the tubules, the thecae slightly glandular, the tubules 2.5–4.5 mm long, dehiscing by clefts 1.5–2 mm long; style 22–29 mm long, exserted at anthesis. *Berry* not seen.

The range of *Psammisia columbiensis* extends from Darién through central and western Colombia to Azuay, Ecuador. The species is characterized by narrow, few-nerved leaves, elongate inflorescences and connate filaments. The few specimens from this wide range show considerable variation and much additional material is needed before a satisfactory circumscription of the species can be made. The material from Panama is incomplete, being vegetatively immature, and lacking an inflorescence, although a single nearly mature flower is found in the packet. This specimen approaches *P. columbiensis* more closely than *P. ramiflora* which is characterized by subfasciculate or short racemose inflorescences and anthers less than 5.5 mm long. *Psammisia ramiflora* is the common species of Costa Rica and central and western Panama. The two species are closely related, however, and are in need of closer study.

DARIÉN: Rain forest, Caná-Cuasí Trail, Chipigana District, 5500 ft, *Terry 1578* (F).

2. **Psammisia darienensis** Luteyn & Wilbur,[5] TYPE: Panama, *Gentry & Mori 14024* (MO, holotype).

Epiphytic *vine*, glabrous throughout except for the filaments; twigs bluntly angled becoming subterete, smooth or slightly striate, brown or grayish brown when dry. *Leaves* subcoriaceous, elliptic to lance elliptic, 16–22 cm long, 6–9

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[5] *Psammisia darienensis* Luteyn & Wilbur, sp. nov. Frutex epiphyticus. Folia elliptica vel lanceolato-elliptica, 16–22 longa et 6–9 cm lata. Racemi axillares, 8–9 floribus. Pedicelli 9–12 mm longi. Calyx 6–6.5 mm longus; lobis 2.5–2.7 mm longis. Corolla cylindrica 7 mm longa. Stamina 10, 6 mm longa; filamentis 1.5 mm longis, pubescentibus; antheris 5.5 mm longis basi rotundatis.

cm wide, basally broadly obtuse or cuneate, shortly decurrent, apically short acuminate, entire, brown when dry, pinnately nerved, the midrib plane or slightly impressed above, conspicuously raised beneath, the 5–7 lateral nerves slightly raised on both the surfaces, anastomosing near the margins, the veinlets slightly raised on both the surfaces; petioles subterete, flattened dorsally, 4–7 mm long, 2 mm in diameter. *Inflorescences* axillary, solitary or paired, racemose, 8–9-flowered; rachis subterete, bluntly angled, 5–7 mm long; floral bracts persistent, coriaceous, ovate lanceolate, acuminate, 2–2.5 mm long, 1.5 mm broad, minutely toothed or glandular fimbriate; pedicels cylindric, striate or ribbed, slightly expanded distally, 9–12 mm long, ca. 0.75 mm in diameter; bracteoles sub-basal, similar to floral bracts but 1.5 mm long, 1 mm broad. *Flowers* slightly beyond anthesis with the hypanthium and the calyx 6–6.5 mm long, the calyx lobes erect, triangular, acute, 2.5–2.7 mm long, the sinuses acute; corolla subcylindric, ca. 7 mm long, 3.5–4 mm in diameter, the lobes triangular, obtuse, 1–1.2 mm long, reflexed at anthesis; stamens 10, conical, 6 mm long, the filaments distinct, ca. 1.5 mm long, 0.75 mm wide, sparsely pilose on the inner surface of the distal half, coarsely ciliate onto the connective margins which become indistinct at the base of the tubules, the connectives neither spurred nor callose thickened, the anthers ca. 5.5 mm long including the tubules, the thecae weakly granular, rounded and broadest at the base, not incurved, the tubules straight, 2–2.3 mm long, dehiscing the length of the tubules by an elongate cleft; style not seen. *Berry* reportedly turning red.

This new species is most closely related to *Psammisia idalima* A. C. Smith which is known only from Ecuador. The two species differ in numerous minor features, which, when combined with their separate ranges strongly suggest distinct entities. *Psammisia darienensis* possesses shorter pedicels (9–12 mm, not 12–20 mm), larger stamens (including longer filaments, anthers and tubules), pubescent filaments and connectives and a dehiscence cleft extending the length of the anther tubule. Also, the shape of the anther is different, the theca-tubule junction being straight in *P. darienensis*, and distinctly geniculate in *P. idalima*; the base of the theca is rounded and not incurved in the new species, while it is tapered and incurved in *P. idalima*. *Psammisia darienensis* also lacks the persistent bracts at the base of the inflorescence which are characteristic of *P. idalima*.

DARIÉN: Top of W ridge of Cerro Tacarcuna, elfin forest and transition between elfin forest and lower montane wet forest, 1800–1850 m, *Gentry & Mori 14024* (MO).

3. **Psammisia dolichopoda** A. C. Smith, Contr. U.S. Natl. Herb. 29: 368. 1950. TYPE: Colombia; Cauca, *Haught 5199* (US, holotype; photo NY).

Epiphytic *shrub*, glabrous except for filaments, mature stems and twigs of the new growth terete or subterete, striate, reddish brown when dry. *Leaves* elliptic, subcoriaceous when dry, (5–)8–14 cm long, (2–)3–5 cm wide, basally cuneate or obtuse, short attenuate, apically long or short acuminate, weakly 5(–7)-plinerved, the midrib, the lateral nerves and the veinlets weakly raised above, more prominent beneath; petiole rugose, 4–5 mm long, 1–2 mm in diameter. *Inflorescence* racemose or subcorymbose, 5–8(–10)-flowered; rachis subterete or

angled, striate, 1.5–4 cm long, the peduncle 1–2 cm long; pedicels terete, striate, (20–)25–30 mm long at anthesis, lengthening to 40 mm post anthesis; floral bracts and the bracteoles minute, ovate, acute to acuminate, 0.5–1 mm long, fimbriate. *Flowers* with the hypanthium and calyx 5–5.2 mm long, obscurely articulate with the pedicel but without a clearly marked groove; the tube cylindric or slightly ribbed, ca. 3 mm long, 5 mm in diameter, the limb campanulate, 2.2–2.5 mm long including the calyx lobes, the lobes short-triangular, ca. 1.2 mm long, the sinuses broadly rounded or flat; corolla subglobose to urceolate, coriaceous, green when fresh, 5.5–6 mm long, 4–5 mm diameter, the lobes triangular, acute, ca. 1.2 mm long; stamens 4–5 mm long, without spurs but the connective broadly callose thickened, the filaments distinct, 1–2.5 mm long, 0.8–1 mm wide, attached to the upper part of the anther sac, ciliate or strigose along the dorsal surface, the anthers 3.5–4.5 mm long, the thecae coarsely granular, 2–3 mm long, tubules 1–1.5 mm long, dehiscing by elongate pores 0.5–0.7 mm long; style inserted, 4 mm long. Mature *berry* not seen.

The extension of the range of *P. dolichopoda* from the type locality in wet montane forest (2,500 m) to the tropical moist forest of the El Llano-Cartí area is surprising. The Panamanian material differs from that of the type collection in seemingly insignificant characters, e.g. rachis 6–8 cm long and corolla 7–9 mm long in the type collection vs. rachis 1.5–4 cm long and corolla 5.5–6 mm long in the Panamanian material.

PANAMÁ: El Llano-Cartí Road, 7–12 km from Interamerican Highway, 360–410 m, *Croat 25160* (DUKE, MO), *26062*, *26076*; *D'Arcy 10606*; (all MO). *Dressler 4674* (DUKE); *Gentry 5798* (DUKE, MO); *Mori 7752* (DUKE, MO); *Mori & Kallunki 2301*, *2903*, *4714* (all MO). DARIÉN: Ascent of Cerro Pirre from Río Pirre S of El Real, 750–1030 m, *Duke 5323* (MO). Cloud forest and mossy forest, Cerro Pirre, 2500–4500 ft, *Duke & Elias 13764* (DUKE, MO).

4. **Psammisia panamensis** A. C. Smith, Ann. Missouri Bot. Gard. 28: 440. 1941.
TYPE: Panama: *Allen 2152* (A, holotype).

Epiphytic *shrub* 0.5–1.0 m high, glabrous throughout except for the filaments; branchlets thick, terete. *Leaves* coriaceous when dry, oblong lanceolate to narrowly elliptic, 26–37 cm long, (3.5–)5.5–9.3 cm wide, basally cuneate, apically acute to gradually acuminate, entire and narrowly revolute, pinnately nerved, the midvein and the principal veins moderately elevated above, prominently so beneath, the veinlets reticulate and conspicuous; petioles rugose, 8–12 mm long, 3–4 mm in diameter. *Inflorescences* axillary, shortly racemose or corymbose at anthesis, 6–10-flowered with practically no peduncle; rachis 6–10 mm long, angled; pedicels 8–12 mm long, 1–1.5 mm in diameter, each subtended by a papery, ovate to deltoid, acute, usually minutely toothed bract 1.5–3 mm long and with 2 submedial, often toothed bracteoles 1.5–2 mm long. *Flowers* with the hypanthium and the calyx broadly campanulate at anthesis, 7–8 mm long, 5–7 mm in diameter at its summit, clearly disarticulating from the pedicel by a sharply delineated groove, the calyx limb slightly coriaceous, suberect, ca. 3 mm long including the lobes, the calyx lobes deltoid, acute, 2–2.5 mm long, basally 2–3 mm wide; corolla glabrous, somewhat fleshy, truncately conic at

anthesis, 6–10 mm long, at the base 5–8 mm in diameter, contracted apically, the lobes 5, deltoid, acute, 1–1.2 mm long and wide; stamens 10, the filaments submembranaceous, distinct, ligulate, 1.5–2 mm long, puberulent ciliolate, apically tapering, the connectives either alternately obscurely 2-spurred and spurless or all spurless, the anther sacs rigid, 3.5–4 mm long, the base conspicuously incurved each with 2 cylindric-conical, connate tubules 1.5–2 mm long which dehisce introrsely by elongate oval clefts about as long as the tubules; stigma ca. 0.5 mm in diameter when receptive. Mature *berry* not seen.

This species is known only from the wet montane forests of central and eastern Panama.

COCLÉ: Hills N of El Valle de Antón, 1000 m, *Allen 2152* (A). DARIÉN: Cloud forest and mossy forest, Cuasí-Caña trail between Cerro Campamiento and La Escalera to "Paramo" E of Tres Bocas, *Kirkbride & Duke 1273* (MO). Lower montane rainforest, N slopes of Cerro Pirre, 700–950 m, *Mori & Kallunki 5477* (DUKE, MO). PANAMÁ: Cerro Jefe, *Croat 14441* (MO). Primary forest, Campo Tres, 3 km NE of Altos de Pacora, 500–800 m, *Croat 22752* (MO). Cerro Jefe, 4.6 km beyond peak on road to Altos de Pacora, 600 m, *Croat 35908* (MO). Altos de Pacora, 20–24 km NE of Cerro Azul, *Dressler 4612* (DUKE, MO). Cerro Jefe, near Río Indio, 2100–2200 ft, *Duke 15211* (MO). Secondary cloud forest, summit of Cerro Jefe, *Dwyer et al. 5045* (MO). Road beyond Cerro Jefe, *Foster 1486* (DUKE). Top of Cerro Jefe, *Gentry 4871* (DUKE, MO). Cloud forest, Altos de Pacora, 680–710 m, *Kennedy & Dressler 3512* (F). Premontane rainforest, 5–10 km NE of Altos de Pacora, 750 m, *Mori & Kallunki 4966* (MO). Caña, 5000 ft, *Williams 966* (NY). VERAGUAS: Primary forest on Caribbean slope above Río Primero Brazo 5 mi NW of Santa Fé, 700–1200 m, *Croat 23138* (DUKE, MO). 2.6 km from Escuela Agrícola Alto de Piedra, NW of Santa Fé, *Mori & Kallunki 4741* (MO). Lower montane wet forest 6–7 km W of Santa Fé on new road past agriculture school, *Nee 9874* (MO).

5. **Psammisia ramiflora** Klotzsch, Linnaea 24: 44. 1851. TYPE: "in locis alpestribus Veraguae Americanae centralis," *Warscewicz* (B, holotype, not seen; photo F, GH, NY).—FIG. 14.

P. symphystemona Donnell Smith, Bot. Gaz. (Crawfordsville) 20: 291. 1895. TYPE: Costa Rica: Prov. de Alajuela: Mariposa, 5500 ft, *Cooper 5842* (US, holotype; GH, US, isotypes; photo, NY).

Usually epiphytic *shrubs* with slender, terete, glabrous branchlets. *Leaves* oblong or ovate oblong, 8–19(–27) cm long, 3–7(–11) cm wide, basally cuneate to rounded, apically caudate acuminate, the tip often 2–4 cm long, entire, glabrous both above and below, 5-plinerved with the secondary nerves originating slightly above the base and ascending near the margins, the midvein slightly impressed or flush above and prominently elevated beneath, the veinlets conspicuously reticulate and elevated on both the surfaces but especially so beneath; petioles rugose, (3–)5–12(–17) mm long, glabrous, narrowly winged above. Inflorescence axillary, subfasciculate or short racemose, 4–15-flowered, the rachis less than 1 cm long, in fruit 1–4 cm long, glabrate throughout; pedicels slender, striate, 8–25 mm long, each subtended by an oblong or triangularly deltoid, persistent bract (1–)3–4 mm long and with 2, usually supramedial, deltoid, persistent bracteoles 1.5–2.5 mm long. *Flowers* with the hypanthium subcylindric or broadly obconic, ca. 3 mm long, 2.5 mm in diameter at the summit, glabrous, the calyx limb 3.5–4.5 mm long including the lobes, the lobes 5, triangular, acute, ca. 1.5 mm long; corolla subcylindric, red with a white tip, 20–35 mm long, 6–10

FIGURE 14. *Psammisia ramiflora* Klotzsch.—A. Habit (×2/5).—B. Inflorescences (×2/5).—C–D. Stamens.—C. Lateral view (×3).—D. Ventral view (×3). [After *Utley & Utley 4453* (DUKE), Costa Rica.]

mm in diameter medially and near the base, contracted above to 4–5 mm in diameter before the elongate throat, the throat often with appressed glandular trichomes 0.1–0.4 mm long, the corolla lobes oblong, 2.5–3.5 mm long; stamens 10 (or in the rare 6-parted flowers, 12) 8–10 mm long, the filaments membranous, brown, 3.5–4.5 mm long, connate for their entire length or sometimes lightly coherent near the base or completely separate and leading into the connectives, the connectives narrow, ciliate with trichomes ca. 0.2 mm long, distally and alternately unequally 2-spurred, the anther sacs 3–3.2 mm long opening into pairs of tubules, the tubules, cylindric conic, 2–3 mm long, weakly coherent or

distinct to the base, opening introrsely by oval clefts about ¾ as long as the tubules; stigma truncate, the style exserted, 32–37 mm long, glabrous. *Berry* subglobose, 8–10 mm high, 10–13 mm in diameter.

This species, known only from Costa Rica and Panama, exhibits more variation than one would expect even in as variable a group as the thibaudioid ericads. The Chiriquí specimens all closely match the numerous Costa Rican representatives which mainly occur about the Meseta Central and especially in the Cordillera Central. Those specimens from the vicinity of Santa Fé in Veraguas have filaments ranging from weakly coherent to completely separate and their leaves seem more coriaceous with a slightly different venation pattern from the populations from Costa Rica and Chiriquí. The specimens seen from Coclé all have separate filaments. Specimens from Panamá and Darién all seemingly have connate filaments but with leaves slightly different from those from Costa Rica and Chiriquí both in texture and venation.

CHIRIQUÍ: Trail from Paso Ancho to Monte Lirio, upper valley of Río Chiriquí Viejo, 1500–2000 m, *Allen 1503* (GH, MO, NY, US). Cloud forest 1–2 km N of Las Nubes and W of Cerro Punta peak, 5 km NW of Cerro Punta, 2000–2200 m, *Almeda 1536* (DUKE). Rich cloud forests, Las Nubes, 5.5 km NW of Río Chiriquí Viejo, 2200 m, *Busey 665*, *Croat 26447* (both MO). Cerro Colorado Copper Mine Development, 28 mi above San Félix, 9–10 mi above turnoff to Escopeta, 1200–1500 m, *Croat 33197* (MO). Wet river gorge, Río Chiriquí Viejo above town of Cerro Punta, 6000–8000 ft, *D'Arcy 6580* (MO). Bajo Chorro, Boquete, *Davidson 59* (A, F, MO, US). Rain forest, Bajo Chorro, 6000 ft, *Davidson 606*, *607* (both F). Slopes of Cerro Punta, 2000 m, *Gentry 5865* (DUKE, F, MO, NY). Rain forest, Cerro Horqueta, 6500 ft, *Hagen 2026* (A, NY). Premontane forest between Pinola and Quebrada Hondo on Chiriquí Trail towards summit, *Kirkbride & Duke 897* (MO, NY). Cloud forest below Divide on Chiriquí Trail, *Kirkbride & Duke 965* (MO, NY). Las Nubes, 2.7 mi NW of Río Chiriquí Viejo W of Cerro Punta, 2200 m, *Liesner 298* (DUKE, MO). Above Las Nubes, NW of Cerro Punta, 1900–2100 m, *Luteyn 3803* (DUKE); *Mori & Bolten 7252* (DUKE, MO). Finca Collins, Boquete, 5800–6700 ft, *Stern, Eyde & Ayensu 2025* (MO, US). Between Bajo Quiel and Bajo Mono 6 mi NW of Boquete, 1450 m, *Wilbur et al. 12016* (DUKE). Mossy forest, 7000 ft, E of Guadeloupe along the Río Chiriquí Viejo 2 mi NE of Cerro Punta, *Wilbur & Teeri 13100B* (DUKE, MO). Wet mossy forest 7500 ft on NW side of Cerro Punta beyond Las Nubes, *Wilbur & Teeri 13221* (DUKE, F, LL, MICH, MO, PMA). COCLÉ: Hills N of El Valle de Antón, 1000 m, *Allen 2192* (A, MO), *2337* (MO). Trail to Cerro Pilón WEPCOR weather station, 1 km from top, 900 m, *Correa 47* (FSU, SCZ). Cloud forest at La Mesa above El Valle, *Croat 13409* (MO). La Mesa above El Valle, 800 m, *Croat 25347* (DUKE, MO). Road past Furlong's Finca due N of Cerro Pilón, 880 m, *Croat 37551* (MO). Cloud forest on slopes of Cerro Pilón near El Valle, 700–900 m, *Duke 12130* (MO). Cloud forest, El Valle, 800–1000 m, *Duke 13204* (MO). Foothills of Cerro Pilón near El Valle, *Duke & Correa 14691* (MO). Between Cerro Pilón and El Valle, 700–900 m, *Duke & Dwyer 13948* (DUKE, MO). El Valle, *Dwyer 1936* (MO). Cerro Pilón, *Dwyer 8354* (MO, NY). 8.5 mi from El Valle toward La Mesa, *Dwyer 10535* (MO). El Valle de Antón at the foot of Cerro Pilón, ca. 2000 ft, *Dwyer & Correa 8008* (DUKE, MO, SCZ). Cerro Gaítal, Caracoral, 2700 ft, *Dwyer & Correa 8911* (MO). Cerro Pilón, 2700 ft, *Dwyer & Lallathin 8649* (MO). Summit of Cerro Pilón above El Valle de Antón, 2700 ft, *Dwyer et al. 4514* (MO). 2.5 mi W of El Valle, *Gentry & Dwyer 3614* (DUKE, F). La Mesa above El Valle, 1000 m, *Gentry 5654* (MO). La Mesa, N of El Valle, 1000 m, *Gentry 6824* (DUKE, MO). Cloud forest, La Mesa, 800 m, *Kennedy et al. 2089* (DUKE, MO). Cerro Caracoral, elfin forest, *Kirkbride 1103* (MO). Cloud forest 6 mi N of El Valle de Antón, 1000 m, *Luteyn 1158* (DUKE). La Mesa, 2.8–3.4 mi NW of El Valle de Antón, 850–900 m, *Luteyn 4071* (DUKE). Road 8 mi N of El Valle de Antón, *Luteyn & Kennedy 1725* (DUKE). La Mesa 4 km N of El Valle, 875 m, *Nee & Dwyer 9140*, *Nee & Dwyer 9148*, *Nee & Dwyer 9625* (all MO). Cloud forest, along road from El Valle to La Mesa, 2400–2600 ft, *Spellman et al. 584* (DUKE, MO). Near El Valle de Antón, *Stockwell* (DUKE). Above El Valle on road to La Mesa, 2500 ft, *Tyson 6935* (PMA). El Valle de Antón, near La Mesa, 5 mi N of El Valle, *Wilbur & Luteyn 11747* (DUKE). 1000 m on La Mesa below the N rim, *Wilbur et al. 11153*

(DUKE, F, MO, NY, PMA, US). La Mesa 3 km N of El Valle de Antón, 850 m, *Wilbur et al. 15651* (DUKE, MO). N rim of El Valle de Antón near Cerro Turega, 650–700 m, *Woodson & Schery 184* (MO, NY). COLÓN: Trail at end of Santa Rita Ridge Road, 600–800 m, *Mori & Crosby 6432* (MO). DARIÉN: Cerro Pirre, *Bristan 614* (MO). Trail from Pucuro to Cerro Mali, near La Laguna, ridge between Pucuro and Tapalisa Rivers, 820–840 m, *Gentry & Mori 13553* (MO). Cloud forest and mossy forest, Cuasí-Caña Trail between Cerro Campamiento and La Escalera to "Paramo," E of Tres Bocas, *Kirkbride & Duke 1327* (MO, NY). N slopes of Cerro Pirre, 700–950 m, *Mori & Kallunki 5475* (MO). PANAMÁ: Después de La Eneida, 750 m, *Correa et al. 805* (DUKE, F, MO, PMA). Camino de Llano a Cartí, 400 m, *Correa et al. 1889* (DUKE, MO, PMA). 6 mi above Goofy Lake on road to Cerro Jefe, *Croat 15217* (MO). Primary forest along newly cut road from El Llano to Cartí-Tupile 12 mi above Panamerican Highway, 200–500 m, *Croat 22855* (MO), *22865* (DUKE, MO). Summit of Cerro Jefe, *Dwyer et al. 5026* (DUKE). Cerro Azul, 3000 ft, *Goldman 1870* (US). 14–17.5 km on road from El Llano to Cartí-Tupile, 200–500 m, *Kennedy 2498* (F, MO, NY). Lowland cloud forest, between Cerro Azul and Cerro Jefe, 1000 m, *Luteyn 3202* (DUKE, NY), *3210* (DUKE). Top of Cerro Jefe, 3000 ft, *Luteyn & Kennedy 3970* (DUKE). El Llano-Cartí Road, 18.8 km from Interamerican Highway, 350 m, *Mori & Kallunki 5133* (DUKE, MO). Ridge running NE of summit of Cerro Jefe, 1000 m, *Mori & Kallunki 6096* (DUKE). El Llano-Cartí Road, 12.7 km from Interamerican Highway, 350 m, *Mori et al. 4684* (MO). Top of Cerro Jefe, 3140 ft, *Tyson 3587* (FSU, MO, SCZ). Cerro Jefe, *Witherspoon 8549* (MO). VERAGUAS: Forested slopes of Cerro Tute, near Santa Fé, 3000 ft, *Allen 4353* (MO, US). 5 mi W of Santa Fé on road past Escuela Agrícola Alto Piedra on Pacific side of divide, 800–1200 m, *Liesner 881* (DUKE, MO). Santa Fé, subiendo Cerro Tute, *Mendieta 573* (PMA). 8.8 km from Escuela Agrícola Alto de Piedra, *Mori & Kallunki 3230* (DUKE, MO). Forest 6–7 km W of Santa Fé on new road past agriculture school, 2900 ft, *Nee 9794* (DUKE, MO).

15. SATYRIA

Satyria Klotzsch, Linnaea 24: 14, 21. 1851. LECTOTYPE: *Satyria warszewiczii* Klotzsch.

Epiphytic or terrestrial *shrubs*. *Leaves* alternate, coriaceous, usually pli-nerved but rarely pinnately veined, petiolate. *Inflorescence* terminal or axillary, often cauliflorous, racemose or subfasciculate with few to many, often pendent flowers; pedicels minutely bibracteolate, each subtended by a small bract. *Flowers* with the hypanthium subglobose to shortly campanulate, a sharply delineated disarticulation groove at its juncture with the pedicel, the calyx limb flaring or spreading, the lobes (3–4)5, ovate to triangular or merely apiculate; corolla cylindric to narrowly vasiform, the lobes 5, triangular to narrowly oblong, acute; stamens 10 of alternately unequal lengths, shorter than the corolla and usually only about ⅓ as long, the filaments equal and firmly connate into a monadelphous tube for more than half their length, membranous to thinly coriaceous, the anthers dorsally attached near their bases, the anther sacs subcoriaceous, firm, alternately unequal in length and dimorphic with slightly granular thecae, the flaring tubules not sharply differentiated from the anther sacs, opening by oblique clefts; stigma usually truncate, the style filiform and as long as the corolla or slightly exserted, the ovary inferior.

Satyria is a well-marked, largely montane genus of approximately twenty five species ranging from southern Mexico to Bolivia and east to French Guiana.

a. Hypanthium and corolla densely puberulous; filaments glabrous; corolla 10–13(–16) mm long ..... 1. S. *allenii*
aa. Hypanthium and corolla glabrous; filaments ciliate; corolla (15–)17–28 mm long ..... 2. S. *warszewiczii*

1. **Satyria allenii** A. C. Smith, Ann. Missouri Bot. Gard. 28: 451. 1941. TYPE: Panama: *Allen 2367* (A, holotype).

Epiphytic, much branched *shrub* or woody *vine* with branches to 2.5 m long; branchlets thick, subterete, angled when young, somewhat cinereous. *Leaves* coriaceous, glabrous, elliptic oblong (4–)6–10(–16.5) cm long, (2–)3–6(–10) cm wide, basally acute, cuneate or rounded, apically cuspidate, the obtuse acumen to 4 mm long, entire, the margin often conspicuously recurved, 5-plinerved, the interior veins often originating 1–2 cm above the base, with the midvein impressed above and prominently elevated beneath; petioles rugose, glabrous, thickened, 6–10 mm long. *Inflorescences* borne on leafless branches, shortly racemose, 2–6 flowered, the rachis slender, glabrous, 6–10 mm long; pedicels "coral pink," slender, distally slightly swollen, whitish puberulent, (6–)9–12 mm long, the bract oblong ca. 1.5 mm long, usually submedial but occasionally medial or supramedial, the bracteoles 2, inconspicuous, narrowly triangular, appressed, 1.5–2 mm long. *Flowers* with the hypanthium "coral pink," 1–2 mm long and 1–2 (–3) mm in diameter, externally densely spreading puberulent with whitish, persistent trichomes 0.2 mm long; calyx limb spreading erect, ca. 2 mm long, slightly fleshy, the lobes 5, deltoid, acute, ca. 1 mm long, 2.5 mm wide; corolla "coral pink" but distally pure white, densely spreading puberulous throughout, fleshy, cylindric, 10–13(16) mm long, 2–3 mm in diameter basally and at the throat, the lobes 5, acute, ca. 0.7 mm long, 1.3 mm wide; stamens 10, alternately 4 mm long and 4.5 mm long, the filaments glabrous, united in a pale, membranaceous tube 2.5–4 mm long, the anthers alternately 2–3 mm long and 2.3–3.8 mm long, the tubules opening by broad clefts ca. 0.6 mm long; stigma minute, subpeltate, the style slender, 1–2 mm longer than the corolla or equalling it. *Berry* (4–)5–7 (8) mm in diameter, 3–4 mm high, capped by the inflexed, acutely deltoid calyx lobes and with a markedly swollen basal enlargement 3–5 mm in diameter just beneath the disarticulation groove.

COCLÉ: Hills N of El Valle, 1000 m, *Allen 2335* (A), *2336* (MO). La Mesa N of El Valle de Antón, 1000 m, *Allen 2367* (A). El Valle de Antón, 1000 m, *Allen 3415* (F, GH, US). Trail beyond La Mesa towards Los Llano, 800–860 m, *Luteyn 3167* (DUKE). La Mesa below the N rim on forested slopes, *Wilbur 11152* (CAS, DUKE, F, GH, LL, MICH, MO, NY, PMA, US, WIS). PANAMÁ: Cerro Jefe, *Busey & Croat 275* (DUKE, MO); *Correa 716* (MO); *Croat 13029* (DUKE, MO); *Croat 13080* (DUKE, MO); *Duke 8174* (MO), *9397* (MO, US), *9426* (MO); *Dwyer et al. 5026* (DUKE, MO); *Dwyer et al. 7275* (MO); *Dwyer 8256* (MO); *Gentry & Dwyer 3423, 3496* (both DUKE, MO); *Gentry & Mori 13435* (DUKE, MO); *Liesner 583* (DUKE, MO). Cerro Campana, 850 m, *Liesner 599* (DUKE, MO). Cerro Jefe, 1000 m, *Luteyn & Wilbur 4656* (DUKE); *Maas & Dressler 697* (MO). Cloud forest, Cerro Campana, ca. 10 km SW of Capira, *Mori & Kallunki 3582* (DUKE, MO). Cerro Campana, rainforest above Su Lin Motel, *Porter et al. 4208* (MO). E slope of Cerro Jefe, 2700 ft, *Tyson 3380* (GH, MO, SCZ); *Tyson 3530* (MO, SCZ). Cerro Campana, 2500 ft, *Tyson 5327* (FSU, MO, SCZ). Slopes of Cerro Jefe beyond Cerro Azul 5.5 m on road to La Eneida, *Wilbur & Teeri 13644* (CAS, CR, DUKE, F, GH, LL, MICH, MO, NY, PMA, UC, US, WIS). Wind-swept mossy crest, slopes of Cerro Campana, 2700 ft, *Wilbur & Weaver 11294* (DUKE). Slopes of Cerro Jefe beyond Cerro Azul, *Wilbur & Weaver 11376* (DUKE).

2. **Satyria warszewiczii** Klotzsch, Linnaea 24: 22. 1851. TYPE: Panama (?), "in Veragua," *Warszewicz* (B, holotype, not seen).—FIG. 15.

S. *clonantha* Klotzsch, Linnaea 24: 22. 1851. TYPE: Panama (?), "in Veragua," *Warszewicz s.n.* (B, holotype, not seen).

Riedelia warszewiczii (Klotzsch) Kuntze, Rev. Gen. Pl. 2: 384. 1891.
R. clonantha (Klotzsch) Kuntze, Rev. Gen. Pl. 2: 384. 1891.

Epiphytic or terrestrial straggly *shrub*; branches 1–2.5(4) m long, stout, terete, glabrous, grayish to brown or reddish brown. *Leaves* oblong, ovate oblong, lance oblong or elliptic, (6–)10–25(–29) cm long, (2–)4–10(–14) cm wide, basally cuneate, rarely rounded, apically acute to acuminate, entire, slightly revolute, chartaceous to coriaceous, glabrous or rarely inconspicuously glandular strigillose beneath, trichomes 0.2 mm long or less, drying reddish brown; 3–(5)-plinerved, the midvein and the principal paralleling veins either impressed or slightly elevated on the upper surface and prominently elevated beneath, the veinlets drying reticulate slightly elevated on both the surfaces. *Inflorescences* often numerous, pendent, usually cauliflorous, either arising from a low padlike mound or shortly racemose, 3–10(–30)-flowered; rachis striate, glabrous, 5–15 (–40) mm long; glabrous or rarely sparsely puberulent, terete, often distally swollen, 8–20(–25) mm long; bract basal, inconspicuously ciliate, triangular, (1.8–) 2–3(–4) mm long, bracteoles 2, alternate, narrowly triangular, acute, inconspicuously ciliate, 1–1.5(–2) mm long. *Flowers* with the hypanthium glabrous, coriaceous, campanulate, occasionally slightly enlarged at the base. 1.5–2.5 mm high, 3–4.2 mm in diameter at anthesis, the calyx limb drying thinly coriaceous, nearly truncate, slightly flaring, 1.5–2.2(–3.0) mm long including the lobes, the lobes minute, apiculate; corolla usually carnose but often drying as though thinly textured, cylindric or tapering to the slightly flaring throat, occasionally thin waisted with a somewhat swollen base and distally flaring, (15–)17–28 mm long, mostly (2–)3–5 mm in diameter, usually bright red for the basal ¾ and apically white, the lobes acute, oblong, 1–2 mm long; stamens 10, staminal tube 1.5–2(–3.0) mm long glabrous the free portion of the anthers ciliate, the thecae alternately 3.8–5 mm long and 4.8–6 mm long, dehiscing by oval clefts 1.8–2.5 mm long; style 18–30 mm long and usually exserted 2–3 mm beyond the corolla, long persisting. *Berry* often glaucous, 5–6 mm high, 7–8 mm in diameter.

This wide-ranging species is known from southern Mexico south to at least eastern Panama. There is considerable morphological variability in the shape and venation of the leaves and in the size of the flowers. The extremes are strikingly unlike but efforts to subdivide the species have met with failure.

BOCAS DEL TORO: Elfin forest on Chiriquí Trail, E slope of La Zorra to Divide, *Kirkbride & Duke 808* (MO, NY). CHIRIQUÍ: Llanos on slopes of Volcán de Chiriquí Viejo and along Río Chiriquí Viejo, 1200 m, *Allen 976* (F, MO). "New Switzerland," central valley of Río Chiriquí Viejo, 1800–2000 m, *Allen 1388* (GH, NY, US). Cerro Punta, 2000 m, *Allen 3494* (F, GH, MO, US). Between Bambito and Cerro Punta, *Croat 10636* (DUKE, MO). Forested hill N of Audubon Cabin, *Croat 13658* (DUKE, MO). Above San Félix along mining road 18–27 mi from Panamerican Highway, 1200–1500 m, *Croat 33051* (NY). Cerro Colorado Copper Mine development, 28 mi above San Félix, 1200–1500 m, *Croat 33248* (MO). Above Cerro Punta on slope of Cerro Respinga, Bajo Grande, 8000 ft, *D'Arcy 6558* (DUKE, MO). Bajo Chorro, Boquete District, 6000 ft, *Davidson 60* (MO), *80* (F), *608* (MO, US). Boquete, 3800 ft, *Davidson 653* (F, MO). Between Boquete and Cerro Horqueta, *Duke 13722* (DUKE, SCZ). 1.4 km S of Cerro Punta, 1850 m, *Graham 289* (GH). Cerro Punta 2.5 km S of Audubon Cabin, 6000 ft, *Kozlovsky K-11, K-16* (both MO, WIS). Cloud forest, Cerro Horqueta, 5800 ft, *Lewis et al. 538* (MO). Las Nubes, 2.7 mi NW of Río Chiriquí Viejo W of Cerro Punta, 2200 m, *Liesner 303* (DUKE, MO). Cerro Punta, *Lindsay 469* (F,

Figure 15. *Satyria warszewiczii* Klotzsch. Habit (×½). [After *Wilbur & Luteyn 19173* (DUKE).]

MO). Bajo Chorro Trail towards Boquete from Cerro Punta, 7000 ft, *Luteyn 3058* (DUKE). Bajo Mono Trail NW of San Ramón towards headwaters of Río Caldera, 1600–1700 m, *Luteyn 3726* (DUKE). Heavily forested slopes along ridge on W side of Cerro Horqueta, 1700–1800 m, *Luteyn 3761* (DUKE, MO). Las Nubes, 5 km NW of Cerro Punta, 6000–6500 ft, *Mori & Bolten 7251* (MO). Cerro Colorado Copper Mine Rd along continental divide N of San Félix, *Mori & Kallunki 5804* (DUKE, MO), *5904*, 5938 (both MO). Bajo Grande, 1–3 km E of town of Cerro Punta, *Nee 10055* (MO). Forests around Boquete, 1000–1300 m, *Pittier 3014* (US). N facing cliff just S of Boquete, *Stern et al. 1958* (MO, US). Mossy forest E of Guadeloupe 2 mi NE of Cerro Punta Ridge, *Wilbur & Foster 13100* (DUKE, F, MO).

Beyond Las Nubes, *Wilbur & Teeri 13223* (DUKE, MO). Slopes above Río Caldera 3 km beyond Bajo Mano, *Wilbur & Luteyn 19173* (DUKE). Halfway between Cerro Punta and Bambito, *Wilbur et al. 10948* (DUKE, F, GH, MO, NY, PMA). Steep forested slopes NE of Cerro Pando NW of Nueva California, 1500 m, *Wilbur et al. 11016* (DUKE, MO). COCLÉ: Cerro Pilón above El Valle de Antón, 2000–2700 ft, *Dwyer 4568* (DUKE, MO). Cloud forest 3 km NE of El Valle, *Mori & Kallunki 2963* (DUKE, MO). La Mesa, *Nee & Dwyer 9158* (MO). La Mesa 5 mi N of El Valle, 2500 ft, *Tyson et al. 2449* (FSU, SCZ). DARIÉN: Cerro Pirre, *Bristan 538* (DUKE, MO, SCZ). Elfin forest, Cerro Campamento S of Cerro Pirre, *Duke 15673* (MO). Cerro Pirre, 2500–4500 ft, *Duke & Elias 13722* (DUKE, MO). Summit of Cerro Pirre, cloud forest, *Gentry & Clewell 6965* (DUKE, MO). Top of Cerro Mali, *Gentry & Mori 13657* (DUKE, MO). Elfin forest, top of W peak of Cerro Tacarcuna massif, 1800–1850 m, *Gentry & Mori 13978* (DUKE, MO). PANAMÁ: Cerro Campana, 800 m, *Allen 2082* (NY), *3962* (NY, US). Rainforest 15.5 km N of El Llano on road to Cartí, 400 m, *Busey 364* (DUKE, MO). El Llano to Cartí-Tupile road 12 mi above Panamerican Highway, 200–500 m, *Croat 22900* (DUKE, MO). El Llano-Cartí road, 5–6 mi N of Interamerican Highway, 350–375 m, *Croat 34775* (NY). Cerro Campana, *Dressler 4518* (DUKE, F, MO, PMA). Cerro Jefe, 3600 ft, *Duke 8174* (DUKE). Cerro Campana, 800–1000 m, *Gentry 4950* (MO). Forest 4.8 mi N of Panamerican Highway just W of El Llano, *Gentry 5084* (DUKE, MO). Near summit of Cerro Jefe, *Gentry & Dwyer 5525* (MO). Cerro Jefe, cloud forest, 800–1000 m, *Gentry & Mori 13448* (DUKE, MO). 16 km above Panamerican Highway on road from El Llano to Cartí-Tupile, *Kennedy et al. 2440* (MO). Tropical wet forest, 10–12 km N of Interamerican Highway along El Llano-Cartí-Tupile road, *Luteyn & Wilbur 4670* (DUKE); *Mori & Kallunki 2310, 2878, 2923* (all DUKE, MO). Premontane rainforest NE of Cerro Azul, *Mori & Kallunki 3642* (MO). El Llano-Cartí road 20.9 km from Interamerican Highway, *Mori & Kallunki 5583* (MO). El Llano-Cartí road 11–12 km from Interamerican Highway, 300–400 m, *Mori et al. 6878* (MO). El Llano-Cartí road 8–12 mi N of El Llano, 400–450 m, *Nee et al. 8751* (DUKE, MO). Cerro Jefe, 2700–3000 ft, *Tyson et al. 3293* (MO). VERAGUAS: Forested slopes of Cerro Tute, vicinity of Santa Fé, 3000 ft, *Allen 4354* (MO, US). Primary forest on Caribbean slope above Río Primero Brazo, 5 mi NW of Santa Fé, 700–1200 m, *Croat 23121* (MO). 5 mi W of Santa Fé on Pacific side of divide, 800–1200 m, *Croat 23154* (MO), *23155* (DUKE, MO). 3.9–5 mi N of Santa Fé, 500–1000 m, *Gentry 2993* (MO). 5 mi W of Santa Fé on Pacific side of divide, 800–1200 m, *Liesner 938* (MO). Above Santa Fé in Pacific watershed, *Luteyn & Wilbur 4555* (DUKE). On slopes of Cerro Tute NW of Santa Fé, *Mori & Kallunki 4776* (DUKE, MO). 7 km W of Santa Fé, ca. 2900 ft, *Nee 11200* (MO). Forest 3–4 km W of Santa Fé, ca. 2500 ft, *Nee 11270* (DUKE, MO).

16. SPHYROSPERMUM

Sphyrospermum Poepp. & Endlich., Nov. Gen. Sp. Pl. 1: 4. 1835. LECTOTYPE: *S. buxifolium* Poeppig & Endlicher.

Sophoclesia Klotzsch, Linnaea 24: 15, 29. 1851.

Slender, often straggly, epiphytic or terrestrial *shrubs* frequently with pendent branches. *Leaves* usually small and obscurely nerved, coriaceous, subsessile. *Inflorescences* usually few, solitary or rarely paired flowers in the axils of the leaves; pedicels slender, cernuous, distally swollen; bracteoles 2, deciduous. *Flowers* with the hypanthia continuous with the pedicel, subglobose or obconic, the calyx limb suberect, the lobes 4–5; corolla cylindric to campanulate, 4–5-lobed; stamens usually as many or twice as many as the corolla lobes, equal or alternately slightly unequal, the filaments slender, ligulate, the anthers inserted dorsally near the base, membranous, smooth, usually shorter than the filament, the 2 distinct tubules as long as or longer than the locules, opening by oval, introrse clefts; stigma truncate, the style filiform, about as long as the corolla. *Fruit* a subglobose or ellipsoid, berry with a smooth or pubescent, brittle pericarp, dry but becoming succulent at maturity, topped by the persistent

calyx limb and lobes, 4–5 loculed, the partitions soon decaying; ovules numerous, axile but often appearing central or even basal; seeds elongate, striate, the green embryo visible through the endosperm.

Sphyrospermum is a troublesome genus of perhaps 20 species. It ranges from southern Mexico and Haiti to Trinidad and French Guiana, through the highlands of Central America and the Andes of South America to Bolivia.

Literature:

Smith, A. C. 1933. The genera *Sphyrospermum* and *Disterigma*. Brittonia 1: 203–232.

a. Hypanthia pilosulose, strigillose to glabrous or nearly so, the trichomes when present, always slenderly based.
  b. Corolla 4 mm long or longer; hypanthium often moderately to densely pilosulose or puberulous as well as glandularly strigillose.
    c. Leaves suborbicular to oblong ovate, (7–)9–15(–18) mm long; stamens 4 ..... 1. S. *buxifolium*
    cc. Leaves ovate to lance ovate, (15–)20–50 mm long; stamens 4–10, 7(–70) ..... 2. S. *cordifolium*
  bb. Corolla less than 2.5 mm long; hypanthium minutely strigillose but never pilosulose or puberulous ..... 3. S. *standleyi*
aa. Hypanthia densely tuberculate, the modified trichomes with greatly swollen bases ..... 4. S. *tuberculatum*

1. **Sphyrospermum buxifolium** Poepp. & Endlich., Nov. Gen. Sp. Pl. 1: 4. *pl.* 8. 1835. TYPE: Peru, *Poeppig* (B, holotype; P, isotype; photos of both NY).

Sophoclesia nummulariaefolia Klotzsch, Linnaea 24: 30. 1851. TYPE: Colombia; *Moritz 1339* (B, not seen; fragm. NY).

Sphyrospermum Roraimae Klotzsch, Linnaea 24: 36. 1851. TYPE: Guyana, *Schomburgk 975* (B, not seen; fragm. & photo NY).

Sophoclesia cordifolia var. *oophylla* Kuntze, Rev. Gen. Pl. 2: 384. 1891. TYPE: Costa Rica, *Kuntze 2153* (NY, holotype).

Vaccinium pachycardium Standley, Fieldiana, Bot. 18: 883. 1938. TYPE: Costa Rica, *Standley & Torres 51769* (US, holotype).

Epiphytic or terrestrial *shrublets* mostly 1.5–4 dm tall; branches slender, pendent to ascendent, glabrate; branchlets brownish and minutely pale puberulous, glabrescent. *Leaves* coriaceous, suborbicular to oblong ovate, (7–)9–15(–18) mm long, 8–20 mm wide, basally subcordate or rounded, apically rounded or obtuse, marginally entire and slightly recurved, sparsely and inconspicuously pilosulose on both the surfaces but becoming glabrate, also usually inconspicuously glandular strigillose beneath, obscurely 3- to 5-nerved from the base, the veins flush with the surface or slightly raised, obscurely reticulate above; petioles ca. 1 mm long, puberulous to glabrate. Pedicels glabrous to sparingly pilose, slightly and gradually swollen distally, (5–)10–18 mm long. *Flowers* with the hypanthium pilose to glabrate, subglobose, 1–1.5 mm in diameter; calyx limb suberect, short, ca. 0.5 mm long including the lobes, the lobes 4, apiculate and separated by rounded sinuses with a tuft of pilosulose trichomes or glabrous; corolla white to pinkish, submembranous, 4–6 mm long, 1–1.5 mm in diameter, sparsely pilose to glabrous, the corolla lobes 4, narrowly triangular, minute, 0.8–1 mm long; stamens 4, equal, slightly shorter than the corolla, the

filaments either sparsely villose or glabrous, 1.8–3 mm long, the anthers smooth, 1.8–2.5 mm long, the tubules about as long as the thecae. *Berry* subglobose, pilose or glabrous, 4–6 mm in diameter, succulent and whitish with a violet or lavender tinge.

This species ranges from the mountains of Nicaragua south into Bolivia and east into the Guyanas. Distinguishing it from some small-leaved specimens of *S. cordifolium* that have usually been treated as *S. majus* is not easy. A. C. Smith (1933) suggested the possibility that "*S. majus* is a hybrid between *S. buxifolium* and *S. cordifolium*."

CHIRIQUÍ: Disturbed cloud forest at Monte Rey above Boquete, *Croat 15723* (MO). Chiquero, Boquete District, 5500 ft, *Davidson 532* (F, MO). Bajo Mono and Quebrado Chiquero, 1500 m, *Woodson 575* (GH, NY). COCLÉ: El Valle, N rim, 800–1000 m, *Allen 1830* (MO). Cerro Pilón near El Valle, 700–900 m, *Duke 12051, 12081* (both MO). Between Cerro Pilón and El Valle de Antón, 700–900 m, *Duke & Dwyer 13929, 13990* (both MO). El Valle, *Ebinger 1112* (F, MO). La Mesa near Cerro Pilón, El Valle, *Hladik 374* (MO). Trail to La Mesa 4.5 mi beyond El Valle de Antón, *Wilbur & Luteyn 11671* (DUKE, F, MICH, MO, NY). DARIÉN: Headwaters of Río Tuquesa 2 km from continental divide, *Croat 27236* (MO). Elfin forest, Cerro Pirre, 2500–4500 ft, *Duke & Elias 13700* (MO). PANAMÁ: Cerro Campana, *Croat 12152* (MO). El Llano-Cartí highway 19 km N of El Llano, *Dressler s.n.* (DUKE). N of Santa Fé 2 km N of Escuela Agrícola Alto de Piedra, *Mori & Kallunki 2579* (MO). NW of Santa Fé, 8 km from Escuela Agrícola Alto de Piedra, Pacific slopes, *Mori & Kallunki 3934* (MO). Tropical wet forest 16 km NW of Santa Fé on road to Calovebora, *Mori & Kallunki 6143* (MO). Lower montane wet forest 6–7 km W of Santa Fé, 2900 ft, *Nee 9855* (MO). Cut-over slopes 2 km N of Santa Fé towards the continental divide, *Wilbur & Luteyn 19117* (DUKE). Forest near second branch of Río Santa Maria along road from Santa Fé, *Witherspoon & Dressler 8890* (DUKE, MO).

2. **Sphyrospermum cordifolium** Benth., Pl. Hartw. 222. 1846. TYPE: Colombia, *Hartweg 1215* (K, holotype, not seen; BREM, isotype, not seen; photo NY).—FIG. 16.

Sophoclesia cordifolia (Benth.) Klotzsch, Linnaea 24: 29. 1851.
S. subscandens Klotzsch, Linnaea 24: 30. 1851. TYPE: Venezuela, *Moritz 1338* (B, holotype, not seen; fragm. & photo NY).
S. ovata Klotzsch, Linnaea 24: 30. 1851. TYPE: Venezuela, *Moritz 1340* (B, holotype, not seen; fragm. NY).
S. flaccida Seemann, Bot. Voy. Herald 164. 1854. TYPE: Panama; Darién, *Seemann* (K, holotype, not seen; fragm. NY).
Sphyrospermum majus Griseb., Fl. Brit. W.I. 143. 1859.
Sophoclesia major (Griseb.) Benth. & Hook., Gen. Pl. 2: 576. 1876.
S. cordifolia var. *normalis* O. Kuntze, Rev. Gen. Pl. 2: 384. 1891. TYPE LOCALITY: Costa Rica.
S. robusta Rusby, Descr. S. Amer. Pl. 77. 1920. TYPE: Bolivia, *Bang s.n.* (NY, holotype).
S. trinitensis Britt., Bull. Torrey Bot. Club 48: 335. 1922. TYPE: Trinidad, *Britton et al. 1316* (NY, holotype).
S. domingensis Urb. & Ekman, Ark. Bot. 21A(5): 54. 1927. TYPE: Haiti, *Ekman 5219* (B, holotype, not seen; fragm. & photo NY).
Vaccinium valerii Standley, Fieldiana, Bot. 18: 884. 1938. TYPE: Costa Rica, *Standley & Valerio 51853* (F, holotype).
Themistoclesia valerii (Standley) Sleumer, Bot. Jahrb. Syst. 71: 390. 1941.

Epiphytic or terrestrial *shrublets*, mostly 2–6 dm tall, the branchlets densely spreading puberulous, glabrescent. *Leaves* coriaceous, ovate, to lance ovate, (1.5–)2.0–5.0(–7.0) cm long, (10–)15–25(–32) cm wide, basally rounded or subcordate and apically obtuse or rounded to acute, marginally entire and

FIGURE 16. *Sphyrospermum cordifolium* Benth. Habit (×1). [After *Wilbur & Luteyn 19402* (DUKE).]

slightly recurved, moderately puberulous on both the surfaces but becoming glabrate, usually moderately beset with appressed glandular trichomes ca. 0.1 mm long, 3(5)-nerved from the base, the midvein and the paralleling principal veins often impressed above and elevated beneath, the veinlets usually obscure; petioles glabrous to pilosulose, 1–2(–3) mm long; pedicels 1(–2) per axil, pilosulose and often with inconspicuous, glandular, appressed trichomes distally, sometimes glabrous, (1.0–)1.5–2.5 cm long. *Flowers* with the hypanthium usually moderately spreading pilosulose, occasionally sparingly so or glabrous, usually appressed glandular strigose proximally, subglobose or thickly fusiform to shortly cylindric, 1–1.5(–2) mm long, 1.0–1.5 mm in diameter; calyx limb erect, 1.0–1.6 mm long including the lobes, the lobes 4 or 5, deltoid, acute, 0.5–0.8 mm long, often with a tuft of trichomes at the tip; corolla membranous, (4–) 5–7(–8) mm long, 1.2–2.0(–2.2) mm in diameter, glabrous or sparsely and inconspicuously strigillose or puberulous distally, the lobes 4 or 5, narrowly triangular, acute, erect; stamens usually either 4–5 or 8–10, slightly shorter than the corolla, the filaments slender, pilosulose or glabrous, 2.0–3.5(–4.5) mm long, the anthers 2–3 mm long, the tubules distinct, about as long to almost twice as long as the thecae. *Berry* subglobose to thickly fusiform, pilosulose or glabrous, white or white with a violet tinge at maturity, fleshy, 4–7 mm in diameter; seeds elongate, whitish, the green embryo visible within.

This species ranges from the mountains of southern Mexico and Hispaniola south into northern South America and along the Andes into Bolivia. It ranges east to French Guiana.

It has been customary to recognize at least two species within this complex but *Sphyrospermum majus* can be distinguished from *S. cordifolium* only by its different stamen number. *Sphyrospermum majus* has 4 or 5 stamens and *S. cordifolium* has 8 or 10. This distinction is not absolute as flowers are encountered with all numbers between 4 and 10. This is an unlikely basis for maintaining two separate taxa; suggested differences in pubescence, corolla size and the ratio of tubule to thecae length all intergrade.

Perhaps to be included here under the binomial *S. cordifolium* are several specimens of *Sphyrospermum* with basally tapering, elliptical leaves, but these may represent an undescribed species. The available specimens are incomplete; they are identified below by an asterisk (*).

BOCAS DEL TORO: Mossy forest-cloud forest, E slope of La Zorra to divide, *Kirkbride & Duke 807* (MO). CHIRIQUÍ: Trail N of Cerro Punta, *Croat 10520* (MO, SCZ). Rain forest, Bajo Chorro, Boquete, *Davidson 196* (A, F, MO). Trail beyond Las Nubes to about midway between Cerro Picacho and Cerro Punta, NW of town of Cerro Punta, 1900–2200 m, *Luteyn & Wilbur 4642* (DUKE, F, MO). Roadsides, pastures and remnants of lower montane wet forest, Bajo Grande, 1–3 km E of the town of Cerro Punta, 2000–2200 m, *Nee 10036* (DUKE, MO). Cloud forest, Finca Collins, *Stern et al. 1105* (GH, MO). Boquete Trail, 6 mi E of Cerro Punta, 7000 ft, *Tyson 7212* (DUKE). Chiriquí Viejo Valley, *White 82* (GH, NY). W of Las Nubes, 5 km NW of Cerro Punta and towards Cerro Picacho, 2000–2100 m, *Wilbur & Luteyn 19357* (DUKE), *19402* (DUKE, MO). Valley of the Río Chiriquí Viejo, E of Guadelupe, 6500 ft, *Wilbur et al. 13039* (DUKE, PMA). COCLÉ: Forest at La Mesa above El Valle, ca. 800 m, *Croat 25348* (MO). DARIÉN: Between Upper Río Membrillo and Camp 7 on the Construction Road to San Blas, 100–800 m, *Duke 10928** (MO). Cloud forest and/or mossy forest, Cerro Pirre, 2500–4500 ft, *Duke & Elias 13795* (MO). Summit of Pico Tacarcuna, 1850 m, *Gentry et al. 16913* (MO). PANAMÁ: Moist upper regions of

Cerro Campana, 1000 m, *Allen 2421* (A). Primary forest along El Llano-Cartí-Tupile road 12 mi from Panamerican Highway, *Liesner 1230* (MO). Cloud forest, Cerro Campana, 850 m, *Luteyn 3979* (DUKE). Premontane wet forest, El Llano-Cartí Road, 12 km N of Panamerican Highway, 400 m, *Nee & Dressler 9365** (MO). VERAGUAS: Primary forest on Caribbean slope above Río Primero Brazo, 5 mi NW of Santa Fe, 700–1200 m, *Croat 23162* (MO). Rio Segundo Brazo, 8 km beyond Escuela Agrícola Alto Piedra beyond Santa Fe, *Croat 25566* (MO). Tropical wet forest on Atlantic slope along Río Dos Bocas 11 km from Escuela Agrícola Alto de Piedra, *Mori & Kallunki 3186* (MO). NW of Santa Fe, 8.8 km from Escuela Agrícola Alto de Piedra, Pacific slope, *Mori & Kallunki 3937, 3982* (both MO). First branch of Río Santa Maria, S of river along road from Santa Fe, *Witherspoon & Dressler 8925** (MO).

3. **Sphyrospermum standleyi** A. C. Smith, Brittonia 1: 210. 1933. TYPE: Costa Rica: Cartago; near Orosi, *Standley 39622* (US, holotype, not seen; photos DUKE, NY).

Straggly, epiphytic or terrestrial *shrub* 4–6(10) dm tall with subrugose and cinereous branchlets. *Leaves* subcoriaceous, ovate to lance ovate, 4.5–6 cm long, 2–2.8 cm wide, basally rounded or obtuse, apically obtuse, entire, either 5-nerved from the base or 5-plinerved, the midvein and secondary nerves flush above slightly impressed and elevated beneath, the veinlets obscure or slightly raised beneath; petioles subterete, 1.5–2 mm long. *Inflorescence* of axillary or cauliflorous, solitary or paired flowers; pedicels 7–15 mm long, swollen distally. *Flowers* with the hypanthium campanulate, strigillose with dark trichomes 0.1 mm long but neither pilose nor puberulent, slightly 4-angled, 1–1.5 mm long, 1.5 mm in diameter, the calyx limb suberect, 0.8 mm long including the lobes, the lobes 4, apiculate; corolla membranaceous, short cylindrical, 2–2.3 mm long, 1 mm in diameter, the corolla lobes 4, deltoid, acute, ca. 0.3 mm long; stamens 4, slightly shorter than the corolla, the filaments stramineous, ca. 1.2 mm long, the anthers membranaceous, ca. 1 mm long, the tubules as long as the anther sacs. *Berry* white, subglobose, 3–5 mm in diameter.

This little collected and poorly understood species is known from a few collections made in central Costa Rica and in eastern Panama.

DARIÉN: Cerro Tacarcuna massif on westernmost ridge and Pico Tacarcuna, 1650–1800 m, *Gentry et al. 16914* (NY).

4. **Sphyrospermum tuberculatum** Wilbur & Luteyn.[6] TYPE: Panama, *Witherspoon 8830* (MO, holotype).

Epiphytic *shrub*; branches terete, striate, fissured, grayish, glabrous. *Leaves* coriaceous, broadly elliptic, 1.8–5.1 cm long, 1.2–2.8 cm wide, basally rounded to obtusely cuneate, apically rounded, entire, glabrous but inconspicuously glandular strigillose on both surfaces, more so beneath, obscurely 3-plinerved; petioles glabrous, 2–3 mm long. *Inflorescence* of solitary or paired flowers in the leaf axils; pedicels pendent, arching in both young and older fruit, 6–8 mm

[6] *Sphyrospermum tuberculatum* Wilbur & Luteyn, sp. nov. Frutex epiphyticus. Lamina foliorum coriacea, elliptica, apice et basi rotundata, 1.8–5.1 cm longa et 1.2–2.8 cm lata, margine integra; petiolo glabro, 2–3 mm longo. Hypanthia tuberculata, ca. 2.5 mm alta et 2–2.2 mm diametro; lobis calycis 5, glabris, 0.4–0.5 mm longis.

long, with dense bulbous based trichomes at least distally; bract triangular, appressed, ca. 0.6 mm long, bracteoles triangular, alternate, 0.3–0.5 mm long, nearly basal. *Flowers* with the hypanthium densely tuberculate with bulbous-based, glandular protuberances, ca. 2.5 mm high, 2–2.2 mm in diameter; calyx limb glabrous, erect to slightly spreading, 0.5–0.7 mm long including the lobes, the lobes 5, erect, triangular, glabrous, 0.4–0.5 mm long. *Fruit* a globose, densely tuberculate white berry; seeds cuneiform with a striate, transparent (when dry) outer layer exhibiting the green embryo within.

This new species is known from a single specimen consisting of three twigs. The dense hypanthial covering of tuberculae is like that of no other species of *Sphyrospermum* known to us.

VERAGUAS: 2 km N of Cerro Tute, *Witherspoon 8830* (MO).

17. THEMISTOCLESIA

Themistoclesia Klotzsch, Linnaea 24: 41. 1851. LECTOTYPE: *T. pendula* Klotzsch.

Straggly to bushy, often epiphytic *shrubs* or *shrublets*. *Leaves* subcoriaceous to coriaceous, occasionally fleshy, alternate, shortly petiolate; venation obscure. *Inflorescence* axillary, racemose or solitary with one to several flowers, pedicels usually short, subtended by small bracts and bearing usually inconspicuous bracteoles. *Flowers* with the hypanthium continuous with the pedicel, obconic or short cylindric, narrowly 5-winged to the sinuses or bluntly angled, the calyx limb erect to slightly spreading, the 5 lobes acute to acuminate, minute to well developed; corolla ovoid to cylindric, the lobes 5; stamens 4–5 or 8–10, equal or alternately slightly unequal, more than ½ as long as the corolla and often about as long as the corolla tube, the filaments distinct, slender and terete to somewhat flattened at the base, the anthers inserted medially or almost basally, the walls smooth, nearly equal to or only about ½ as long as the tubules, the tubules 1 or 2, if 2, often completely separate, dehiscing by short, introrse clefts; style filiform, about as long as the corolla. *Berry* with numerous small seeds; the green embryo clearly visible through the surrounding tissue.

Themistoclesia is a genus of about 25 species ranging from Costa Rica and Panama through the Andes from Venezuela and Colombia into Peru.

a. Staminal tubules 1 per anther with a single introrse cleft; hypanthium distinctly 5-winged; leaves apically obtuse ..... 3. *T. pentandra*

aa. Staminal tubules 2 per anther, the tubules either separate or united but with 2 introrse clefts; hypanthium bluntly 5-angled, not winged; leaves apically acute or acuminate.

b. Corolla 2.5–3.5 mm long; leaves less than 1.9 cm long, basally tapering or cuneate ..... 4. *T. smithiana*

bb. Corolla 5–6 mm long; leaves more than 2 cm long, basally rounded, subtruncate or subcordate.

c. Bracteoles ovate to hemispheric, completely concealing the glabrous pedicel; corolla cylindric, pilosulose throughout; stamens 5 mm long, filaments pilosulose, anther basally minutely appendiculate ..... 1. *T. costaricensis*

cc. Bracteoles awl-shaped, never concealing the pilosulose pedicel; corolla

urceolate, pilosulose distally; stamens 2.5 mm long, filaments glabrous, anther without basal appendage ..... 2. *T. horquetensis*

1. **Themistoclesia costaricensis** Luteyn & Wilbur, Brittonia 29: 265. 1977. TYPE: Costa Rica, *Luteyn et al. 4407* (DUKE, holotype; F, MO, NY, isotypes).

Pendent, epiphytic *shrub* with branches to 0.5 m long; stems terete, minutely striate, tan to reddish brown when dry, hispidulous with reddish brown trichomes 0.6–0.8 mm long, glabrate with age. *Leaves* distichous, flat or concave, ovate, (1.6–)2–2.5 cm long, (0.8–)1–2 cm wide, basally rounded or subcordate, apically acute or short acuminate, entire, hispidulous above especially near the margins, glabrous beneath, brown above and olive green or light brown beneath when dry; venation obscurely 5-plinerved, the midrib slightly impressed proximally, raised distally above, slightly impressed but inconspicuous beneath, the lateral nerves and the veinlets slightly raised but inconspicuous above, totally obscure beneath; petiole subterete, densely puberulous to pilosulose, 1–1.5 mm long. *Inflorescence* of axillary, solitary flowers with 4 minute basal inflorescence bracts; floral bract ovate, ciliate, ca. 1.5 mm long; pedicel terete, glabrous, 1–2 mm long, completely concealed by the bracteoles; bracteoles 2, ovate to hemispheric, distally hispidulous. *Flowers* with the hypanthium glaucous, copiously pilosulose with translucent or reddish tinged trichomes 1–1.2 mm long, the tube obconic, bluntly 5-angled, ca. 3 mm long; calyx limb 1–1.5 mm long including apiculate lobes; corolla cylindric, narrowed at the throat, 5–6 mm long, ca. 2.2 mm in diameter near the base, pilosulose throughout, white, the lobes ca. 1 mm long; stamens 10, ca. 5 mm long, the filaments alternately 2.8–3 mm and 3–3.2 mm long, pilosulose over the entire length, the anthers ca. 2.5 mm long, the tubules slightly longer than the thecae, the theca with a minute, 0.1 mm long, fingerlike appendage protruding from the base; style 5–6 mm long, glabrous. *Berry* not seen.

Themistoclesia costaricensis is known from Serranía del Darién and from Costa Rica. The identity of the Panamanian specimen is not certain as the material is immature, and there are discrepancies between it and specimens from the type locality along the Río Grande de Orosi in central Costa Rica. These differences include cauline trichomes 0.8–1.2 mm long vs. 0.6–0.8 mm long, leaves to 3 cm long vs. 1.6–2.5 cm long, bracts and bracteoles glandular fimbriate vs. ciliate, and pedicels sparsely pilosulose vs. glabrous.

DARIÉN: summit of Pico Tacarcuna, highest point of the Serranía del Darién, 1850 m, *Gentry et al. 16911* (NY).

2. **Themistoclesia horquetensis** Luteyn & Wilbur, Brittonia 29: 266. 1977. TYPE: Panama; Chiriquí, S slope of Cerro Horqueta, 2,200 m, *Wilbur et al. 13491* (DUKE, holotype).

Epiphytic *shrub* ca. 5 dm tall; stems subterete or bluntly angled, minutely striate but becoming smooth, glaucous, pale reddish brown when dry, hispidulous with translucent trichomes 0.2–0.3 mm long, glabrous with age. *Leaves* distichous, ovate, (2.5–)3–4.5 cm long, 1.5–2.5 cm wide, basally broadly rounded or subtruncate, apically short acuminate, apiculate, entire, obscurely short pilose

above, especially near the margins, glabrous beneath, pale green above, brown beneath when dry but with a pale greenish brown area 1 mm broad along the entire margin; venation 3(–5)-plinerved, the nerves obscure but slightly impressed above, only the midrib slightly raised beneath; petiole subterete, flattened above, 2–3 mm long and 1 mm diameter, hispidulous with translucent trichomes 0.2–0.3 mm long. *Inflorescence* of axillary, solitary flowers, bracts 2–4, minute, basal; floral bract ovate, ciliate, 0.3–0.5 mm long; pedicels angled, striate, glaucous, hispidulous, 1.5–2.5 mm long; bracteoles awl-shaped, ciliate, ca. 0.5 mm long, supramedial. *Flowers* with the hypanthium glaucous, sparsely hispidulous with translucent hairs ca. 0.2 mm long, the tube obconic, bluntly 5-angled, 2–3 mm long; calyx limb 1.5–1.7 mm long including the apiculate lobes; corolla urceolate, strongly constricted at the throat, 5–5.5 mm long, ca. 2.2 mm diameter near the base, glabrous below, the upper part of the throat and the lobes hispidulous, the lobes ca. 0.5 mm long; stamens 10, 2.5 mm long, the filaments alternately 1.5 and 2 mm long, glabrous, the anther 1–1.2 mm long inserted near the base, the tubules equaling the thecae; style ca. 3.5 mm long, glabrous. *Berry* ca. 5 mm in diameter.

This species is known only from the holotype.

CHIRIQUÍ: S slopes of Cerro Horqueta, N of Boquete, 2200 m, *Wilbur et al. 13491* (DUKE).

3. **Themistoclesia pentandra** Sleumer, Bot. Jahrb. Syst. 71: 392. 1941. TYPE: Costa Rica, Prov. de Cartago, La Estrella, *Standley 39374* (US, holotype).

Epiphytic, often slender and straggly *shrub* 3–6(–15) dm tall with ascendent branches; stems terete, striate, fissured, grayish to brown or reddish brown, moderately to densely spreading short pubescent or pilosulose with hyaline trichomes 0.2–0.6 mm long, glabrate with age. *Leaves* spirally arranged, elliptic to oblong elliptic, (1.5–)2.0–3.5(–4.5) cm long, (0.8–)1.2–2.0(–2.5) cm wide, basally cuneate, less commonly rounded, apically acute to obtuse, entire, moderately but inconspicuously spreading pilosulose to puberulous on both the surfaces when young, becoming glabrate or more sparsely pubescent, the lower surface also inconspicuously moderately glandular strigillose, obscurely 3–5-plinerved, the midvein and the principal veins slightly elevated above and beneath, the lateral veins obscurely reticulate on both the surfaces; petiole flattened above, pilosulose to puberulous, rugose, 1–2(–3) mm long. *Inflorescence* of axillary, solitary or very rarely paired flowers; bracts 2 or 4, appressed, triangular 1–1.5 mm long; bracteoles 2, appressed, lanceolate, puberulous 1.2–1.5 mm long; pedicels terete, puberulous 1.5–2.5 mm long. *Flowers* with the hypanthium 3.5–4 mm long, conspicuously 4–5-winged, the wings conspicuously ciliate with hyaline trichomes 0.2–0.4 mm long, these trichomes occurring elsewhere on the surface, the surface of the hypanthium sparingly to moderately beset with minute, glandular trichomes; calyx limb 0.8–1.0 mm long including the minute apiculate lobes; corolla sharply pentangular, tapering sharply to the throat, 3–4.5 mm long, basally 2.0–2.5 mm in diameter, moderately hyaline pilosulose throughout, both internally and externally, light orange with a pale

yellow tip, the lobes 4–5, narrowly triangular, acute, 1.0–1.5 mm long, erect or the tips slightly spreading; stamens 5–10, 3.2–3.5 mm long, equal or nearly so, about as long as the corolla tube; filaments glabrous or sparingly ciliate, ca. 1.5 mm long, flattened basally, the anther sacs attached medially, the thecae slightly granular, 1.0–1.2 mm long, the tubules smooth, conical, 1.5–1.8 mm long; stigma truncate, the style 3–3.5 mm long or about as long as the corolla tube. *Fruit* 4–5-winged, the wings 1–2 mm wide, pale greenish, 5–7 mm long.

Themistoclesia pentandra has been rarely collected and specimens seen have been incomplete. It is possible that more than one species is included under this binomial. Most recent collections have 8 or 10 stamens while the original description and indeed the specific epithet indicates 5. The inclusion of *Duke & Elias 13688* from Darién is especially suspect due to the following differences from all other specimens of *T. pentandra*; the calyx is glabrous rather than ciliate, the corolla is glabrous externally and minutely papillose or short puberulous within in contrast to being externally and internally pilosulose, and its stamens, including the filaments, thecae and tubules are all shorter. These differences are significant but we are reluctant to name another species based upon a single, rather incomplete specimen.

CHIRIQUÍ: N of San Félix on Cerro Colorado Copper Mine road along continental divide, 5000–5500 ft, *Mori & Kallunki 5984* (MO). COCLÉ: Cloud forest on slopes of Cerro Pilón near El Valle, 700–900 m, *Duke 12080, 12085* (both MO). Tropical wet forests, La Mesa, 4 km N of El Valle, 875 m, *Nee & Hale 9612* (MO). DARIÉN: Cloud forest and/or mossy forest, Cerro Pirre, 2500–4500 ft, *Duke & Elias 13688* (DUKE, MO).

4. **Themistoclesia smithiana** (Standley) Sleumer, Bot. Jahrb. Syst. 71: 392. 1941.

Vaccinium smithianum Standl., Fieldiana, Bot. 18: 833. 1938. TYPE: Costa Rica, *Standley & Valerio 51858* (F, holotype; US, isotype).

Pendent to spreading, epiphytic *shrublet* mostly 2–3(–4.5) dm tall; stems terete, slender, brown or reddish brown to grayish when dry, densely to moderately pilosulose with hyaline trichomes 0.2–0.5 mm long, maturing to glabrate. *Leaves* thickly coriaceous, distichous, concave, lanceolate to ovate lanceolate, (0.7–) 1.0–1.5(–1.8) cm long, (3.0–)6.0–8.0 mm wide, basally acute to rounded, apically acute to acuminate, entire, inconspicuously but copiously pilosulose above when young becoming glabrate, the trichomes slender, spreading, ca. 0.2 mm long, beneath glabrous except for reddish brown, minute, glandular trichomes 0.1 mm long or less; venation obscure above except the midvein sunken above and completely obscured beneath; petiole terete, densely hispidulous, 0.5–1.5 mm long. *Inflorescences* of axillary, solitary flowers; bracts several, basal; floral bract ovate, pilosulose, ca. 0.8 mm long; pedicel terete, pilosulose, 1.0–1.2 mm long; bracteoles linear to linear oblong, reddish brown, pilosulose, 0.4–0.6 mm long. *Flowers* with the hypanthium copiously pilosulose with hyaline trichomes 0.3–0.6 mm long, the tube obconic, terete, ca. 2.5 mm long at anthesis; calyx limb ca. 0.7 mm long, the triangular, acute lobes 1.2–1.5 mm long; corolla pale yellow to pale greenish white or white, terete or obscurely 5-lobed, broadly ovoid, abruptly narrowed at the throat, 3–3.5 mm long, 2.5–3 mm in diameter near the base and 0.8–1.0 mm in diameter at the throat,

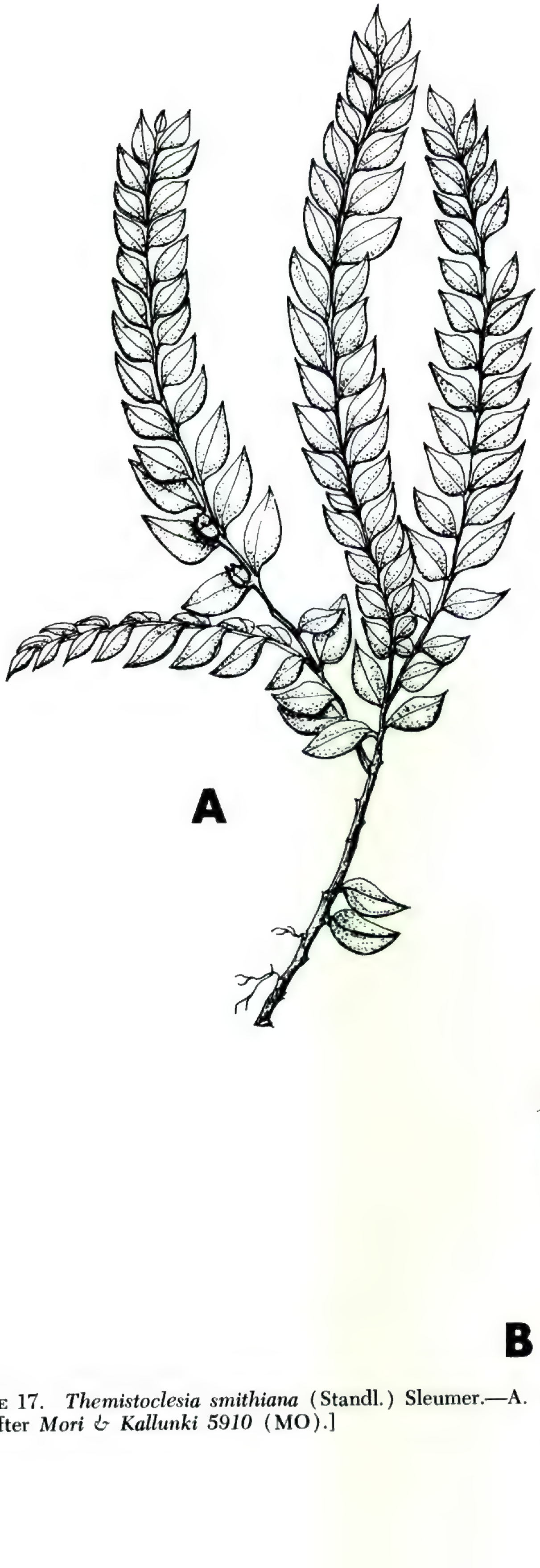


FIGURE 17. *Themistoclesia smithiana* (Standl.) Sleumer.—A. Habit (×⅘).—B. Flower (×8). [After *Mori & Kallunki 5910* (MO).]

glabrous for the basal ⅘, pilosulose distally, the lobes linear oblong, 0.5–0.8 mm long, erect or weakly flaring; stamens 10, equal, ca. 2.5 mm long or about as long as the corolla tube, the filaments slender, terete, glabrous, attached medially to the back of the anther sac, the anther ca. 1.5 mm long including the tubules, smooth, the 2 separate tubules on each anther 0.8–1.0 mm long and dehiscing by an introrse cleft ca. 0.6 mm long, the thecae smooth, 0.6–0.8 mm long, straight; style ca. 3 mm long. *Berry* inconspicuously angled, 5–7 mm long, ca. 4 mm in diameter, bluish.

The distinctive but easily overlooked *T. smithiana* is known only from central Costa Rica and from western Panama.

CHIRIQUÍ: Cloud forest N of San Félix at Chiriquí-Bocas del Toro border, on Cerro Colorado copper mine road along the continental divide, *Mori & Kallunki 5910* (MO). VERAGUAS: On ridgetop in cloud forest, Cerro Tute 10 km NW of Santa Fé, above 1000 m, *Mori et al. 7592* (MO).

18. THIBAUDIA

Thibaudia Ruiz & Pavón ex St. Hil., Expos. Fam. 1: 362. 1805. LECTOTYPE: *T. mellifera* Ruiz & Pavón ex St. Hil.

Eurygania Klotzsch, Linnaea 24: 15, 26. 1851.

Epiphytic or terrestrial *shrubs*. *Leaves* coriaceous or subcoriaceous, pinnately veined or plinerved, petiolate. *Inflorescence* axillary or terminal, subfasciculate, racemose or paniculate with few to many flowers borne on deciduously bibracteolate pedicels articulated with the flowers or rarely continuous (in one South American section). *Flowers* with the hypanthium short cylindric or campanulate, wingless or occasionally narrowly 5-angled to the sinuses (South America); calyx limb erect to slightly spreading distally, the lobes 5, triangular, subacute; corolla subcylindric, occasionally 5-angulate, the lobes 5, triangular or oblong, subacute; stamens 10, equal, often nearly as long as the corolla, the filaments distinct (Central America) or connate (some South American species), the anthers dorsally attached near the bases, firm or membranous, the thecae smooth or slightly granular, the tubules as long as the anther sacs or rarely twice as long, opening by elongate introrse clefts; style filiform, as long as the corolla or slightly exserted; ovary inferior. *Fruit* a berry.

Thibaudia is a genus of about 60 species with one species in Panama and Costa Rica and the others ranging from Colombia to Peru and eastward to Mt. Roraima on the Venezuela-Guayana border.

1. **Thibaudia costaricensis** Hoerold, Bot. Jahrb. Syst. 42: 311. 1909.—FIG. 18.

Usually epiphytic *shrubs*; branches elongate to 2 m long; branchlets terete, cinereous, glabrous. *Leaves* chartaceous or thin coriaceous, oblong or lanceolate oblong, to elliptic, (10–)12–24 cm long, (1.7–)3.5–5(–7.5) cm wide, basally cuneate, apically caudate acuminate, marginally entire and slightly revolute, superficially glabrous or with inconspicuous glandular strigillose trichomes on both the surfaces, 5-plinerved, the secondary nerves originating near the base, the midvein

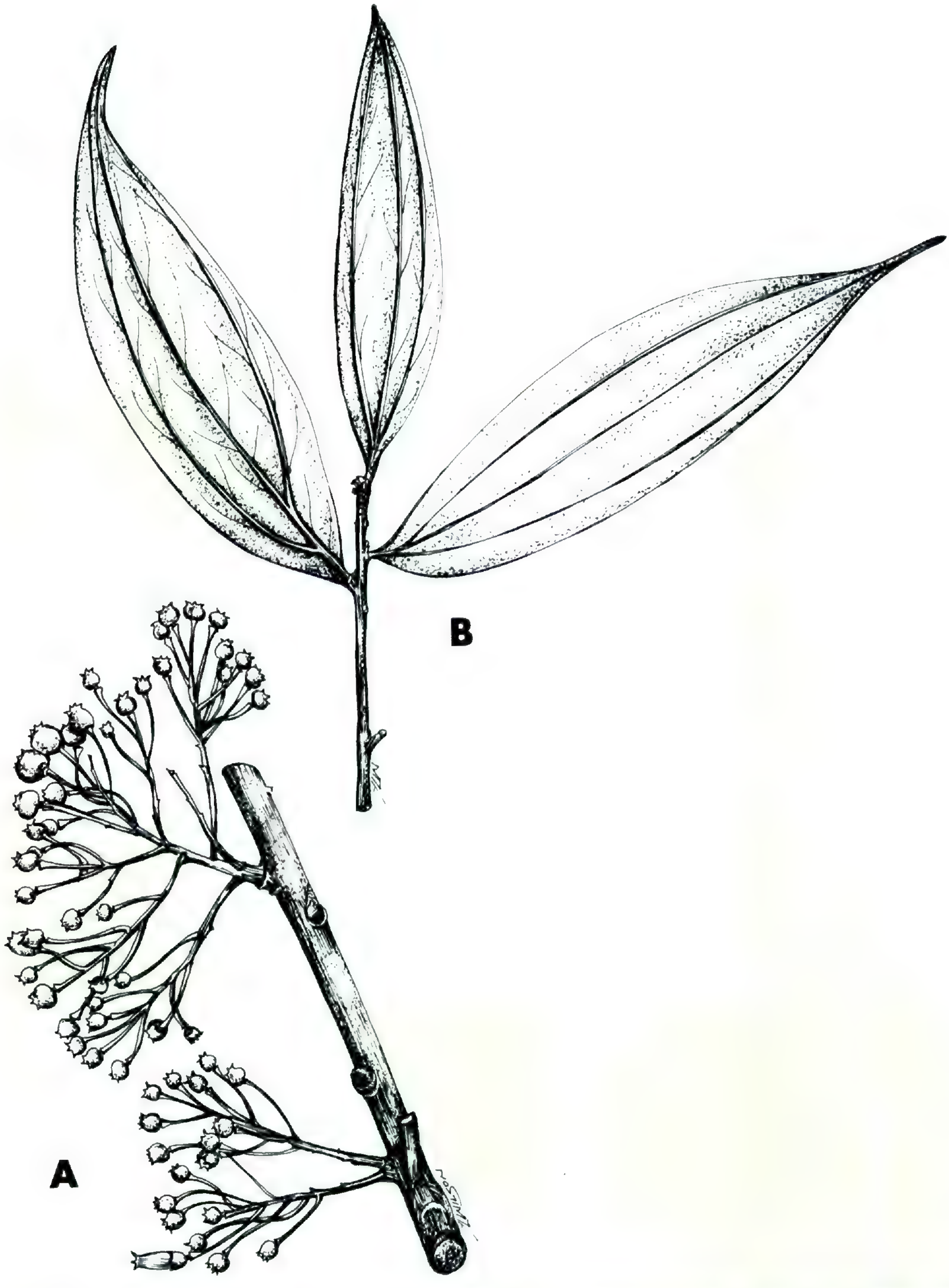


FIGURE 18. *Thibaudia costaricensis* Hoerold.—A. Inflorescences (×3/5).—B. Leafy twig (×3/5). [After *Wilbur & Stone* 8633 (DUKE), Costa Rica.]

impressed above and prominently raised beneath, the veinlets reticulate and slightly raised on both the surfaces; petioles glabrous, 2–3(–4) mm long. *Inflorescences* axillary or cauliflorous, numerous, racemose, or paniculate, 15–30-flowered, the rachis slender, 2–5 cm long, laxly and sparsely puberulous or gla-

brous; pedicel reddish or pinkish, subterete, glabrous or puberulous, distally slightly swollen, 10–16 mm long; bract minute, deciduous, 1–1.5 mm long; bracteoles 2, submedial, deciduous 0.8–1.2 mm long with a sharply delineated disarticulation groove at the base of the flower. *Flowers* with the hypanthium rugose, sparsely puberulous or glabrous, pinkish to roseate, ca. 2 mm long, 2.5 mm in diameter, campanulate, the calyx limb 1–2 mm long including the lobes, erect or spreading, the lobes acute, 0.5–1 mm long, sometimes cartilaginous; corolla tube 9–10 mm long, cylindric, white, 3–3.5 mm in diameter, slightly contracted at the base and at the throat, the lobes 1–1.5 mm long; stamens 10, ca. 7 mm long, equal or almost so; filaments brown, membranous, firmly connate into a glabrous tube 2–3 mm long; anther sacs smooth to slightly granular, ca. 2 mm long, the tubules wide, flexible, completely free ca. 3 mm long opening introrsely by elongate, oval clefts about ½ as long as the tubule; stigma broadly peltate, ca. 1 mm in diameter, the style exserted 1–2 mm at maturity.

This distinctive and relatively uniform species is the only representative of the genus in Central America. It is endemic to the mountains of western Panama and central Costa Rica.

BOCAS DEL TORO: Robalo Trail, N slopes of Cerro Horqueta, 6000–7000 ft, *Allen 4808* (GH, MO, NY, US). CHIRIQUÍ: Bajo Chorro, Boquete District, 6000 ft, *Davidson 380* (A, F, MO, US). Along path in rain forest, Boquete Region, 6500 ft, *Hagen 2023* (A, NY). Premontane rain forest between Pinola and Quebrada Hondo toward summit, *Kirkbride & Duke 880* (MO, NY). Bajo Chorro trail towards Boquete from Cerro Punta, 7000 ft, *Luteyn 3057, 3063* (both DUKE). Heavily forested slopes along ridge on the W side of Cerro Horqueta, 1700–1800 m, *Luteyn 3760* (DUKE).

19. VACCINIUM

Vaccinium L., Sp. Pl. 1: 349. 1753; Gen. Pl., ed. 5. 166. 1754. LECTOTYPE: *Vaccinium myrtillus* L.

Oxycoccus Hill, Brit. Herb. 324. 1756. TYPE: *Vaccinium oxycoccus* L.
Polycodium Raf., Amer. Monthly Mag. & Crit. Rev. 2: 266. 1818 and 4: 189. 1819.
Batodendron Nutt., Trans. Amer. Philos. Soc. II. 8: 261. 1843. TYPE: *B. arboreum* (Marshall) Nutt. (= *V. arboreum* Marshall).
Picrococcus Nutt., Trans. Amer. Philos. Soc. II. 8: 262. 1843. LECTOTYPE: *P. stamineum* (L.) Nutt. = *Vaccinium stamineum* L.
Cyanococcus (A. Gray) Rydb., Fl. Rocky Mts. 645, 1065. 1917. TYPE: *C. pensilvanicus* (Lam.) Rydb. (*pennsylvanicus*) (= *V. angustifolium* Ait.).
Herpothamnus Small, Man. S.E. Flora 1017. 1933. TYPE: *H. crassifolius* (Andr.) Small = *Vaccinium crassifolium* Andr.
Hugeria Small, Fl. S.E. U.S. 896. 1903. TYPE: *Hugeria erythrocarpa* (Michx.) Small (= *Vaccinium erythrocarpum* Michx.)
Rhodococcum (Rupr.) Avorin, Bot. Zurn. SSSR. 43: 1721. 1958. TYPE: *Rhodococcum vitis-idaea* (L.) Avorin (= *Vaccinium vitis-idaea* L.).

Shrubs or rarely *trees*, often rhizomatous. *Leaves* persistent or deciduous, entire or serrate, pinnately veined or rarely plinerved; petioles short. *Inflorescences* racemose, developing from the buds of the previous season, rarely only 1–2 flowered, the flowers borne in the axils of the bracts or the leaves; pedicels usually bibracteolate, either articulated or continuous. *Flowers* with the hypanthium cylindric to globose; calyx lobes (4–)5, rarely obsolete; corolla gamopetalous, white, greenish, red or yellowish, cylindric, urceolate or campanulate,

the lobes 4–5, rarely parted almost to the base; stamens 8 or 10, the anthers lacking awns and with or without dorsal spurs, tapering upward into tubules and opening by a terminal pore or rarely an oblique cleft; pollen in tetrads and without viscin strands; stigma small, simple or somewhat capitate, the ovary completely or partly inferior, 4–5(–falsely 10)-locular, the placentation axile. *Berry* 5 to many seeded, crowned by the persistent calyx lobes and capped by the conspicuous nectariferous disc.

Vaccinium is a genus of perhaps 300 species primarily of the Northern Hemisphere, mostly montane in the tropics. The genus as usually interpreted is diverse and this diversity is amply exhibited by the few representatives found in Central America.

Literature:

Sleumer, H. 1936. Die Arten der Gattung *Vaccinium* L. in Zentral und Südamerika. Notizbl. Bot. Gart. Berlin-Dahlem 13: 111–140.

Standley, P. C. 1920–26. Trees and shrubs of Mexico. Contr. U.S. Natl. Herb. 23: 1–1721.

a. Leaves crenate serrulate; corolla white or white tinged with pink or red; flowers borne in a secund raceme; anthers spurred; calyx and corolla lobes 4 ---------- 1. *V. consanguineum*

aa. Leaves entire; corolla reddish or pale greenish yellow; flowers solitary in the axils of the leaves or borne in an umbelliform cluster; anthers spurless; calyx and corolla lobes 4 or 5.

b. Corolla 4-lobed, red or reddish purple; stamens 8; shrublets creeping, vinelike, closely clasping the bark; hypanthium and pedicel continuous (nonarticulate); flowers solitary ---------- 2. *V. dissimile*

bb. Corolla 5-lobed, mostly pale greenish yellow to yellow but often tinged with pink; stamens 10; erect shrubs or trees, or, if epiphytic, neither creeping nor closely clasping the bark; hypanthium and pedicels jointed (articulate); flowers in corymbose or umbellate racemes.

c. Calyx lobes 5–6 mm long; principal veins of leaves moderately spreading hirsute beneath; hypanthium and calyx lobes both hirsute and with glandular, capitate protuberances ---------- 4. *V. jefense*

cc. Calyx lobes 4 mm or less long; principal veins of leaves at most puberulent or glandular strigillose beneath; hypanthium and calyx lobes glabrous to inconspicuously puberulous.

d. Calyx lobes 2–3.5 mm long; staminal tubules ca. 1 mm long ---------- 3. *V. floccosum*

dd. Calyx lobes 1 mm long or less; staminal tubules 3 mm long or longer.

e. Staminal tubules 3.5–5.5 mm long, each dehiscing by a terminal truncate or slightly inwardly facing pore; Chiriquí ---- 5. *V. poasanum*

ee. Staminal tubules 3.0–3.2 mm long, each dehiscing by a lateral cleft 2–2.5 mm long; Veraguas ---------- 6. *V. santafeënsis*

1. **Vaccinium consanguineum** Klotzsch, Linnaea 24: 64. 1861. TYPE: Panama, *Warscewicz* (B, not seen and presumably destroyed; photo seen, MO).

V. irazuense Sleumer, Notizbl. Bot. Gart. Berlin-Dahlem 12: 138. 1934. TYPE: Costa Rica: Lavafelder des Irazú, *C. Hoffman 140* (B, not seen and presumably destroyed but fragments seen at US).

V. consanguineum var. *irazuense* (Sleumer) Sleumer, Notizbl. Bot. Gart. Berlin-Dahlem 13: 126. 1936.

Shrubs or small *trees* (0.5–)1–3(–4) m tall, often compact and densely bushy with stiff, rigid, glabrous to densely puberulent branchlets. *Leaves*

pinnately veined, persistent, glabrous or with scattered glandular trichomes beneath and moderately puberulous along the midvein; shallowly serrulate with teeth mostly (1–)2–4 mm apart, each tooth often tipped with a darkish glandular callosity, marginally callose thickened, (1.0–)1.5–3(–4.6) cm long, 5–12(–18) mm wide, usually 2–3 times as long as wide, mostly narrowly to broadly elliptic, occasionally oblong, usually tapering to an acute apex and base; petioles 1.5–3 mm long, glabrous or puberulent. *Inflorescence* an axillary raceme, mostly 1–4 cm long; rachis sharply angled, puberulent; bracts scarious, slightly puberulent or ciliate, ovate to oblong, 2–3 mm long; pedicels puberulent, 1–2 mm long; bractlets subopposite, ovate to oblong, scarious, ciliate but otherwise glabrous, entire to sparingly irregularly and minutely toothed, 1.5–3 mm long. *Flowers* with the hypanthium sharply articulated with the pedicel, campanulate, glabrous, 1–1.6 mm long; calyx limb 0.5–0.7 mm long, the lobes 4, deltoid to broadly ovate, apically ciliate but otherwise glabrous, 0.8–1.5 mm long; corolla cylindric, 5–7.5 mm long, glabrous, creamy white with tinges of red or pink, the tube 4–6 mm long, 3–4 mm in diameter, the corolla lobes 4, oblong, 1–1.7 mm long; stamens 8, the filaments 3–4 mm long, ciliate, the anthers granular papillate, the thecae 1.5–1.8 mm long, each sac with a tubule and 2 spurs, the tubule 1.2–1.8 mm long dehiscing by an introrse cleft 0.5–0.7 mm long, the spurs slender, horn-like, ascendent, originating from near the apex of the thecae, 0.2–0.6 mm long. *Berry* reddish to blackish purple at maturity, globose, 5–6 mm in diameter.

This species was included by Standley (1920–26, p. 1101–1102) as part of the woody flora of Mexico but its presence north of Costa Rica was questioned by Sleumer (1936) and the species was not included by Standley & Williams in the Flora of Guatemala (Fieldiana, Bot. 24: 120–127. 1966). It apparently is restricted to the mountains of western Panama and Costa Rica.

CHIRIQUÍ: Forested ridges S of Finca Lerida, 6000–7000 ft, *Allen 4768* (F, GH, MO, NY, US). Summit and SW face of Cerro Copete, 9000 ft, *Allen 4894* (MO, US). Volcán Barú, on E slopes, along road 1 mi from summit, 3000 m, *Croat 34917* (MO). Road up E slope of Volcán Barú, 8 mi from Boquete, 2300–2400 m, *Croat 35001* (MO). Roadside, Potrero Muleto to summit of El Barú, *D'Arcy 10152, 10170* (both DUKE, MO). E slope of Volcán de Chiriquí, WNW of Boquete, 1900–2000 m, *Davidse & D'Arcy 10165* (DUKE, MO, NY). Oak forest at 2400 m, E slopes of Volcán de Chiriquí, WNW of Boquete, *Davidse & D'Arcy 10204* (DUKE, MO, NY). Volcán de Chiriquí, 7000 ft, *Davidson 868* (A, F, MO, US), *901* (F). Potrero Muleto, Volcán de Chiriquí, 10500 ft, *Davidson 1034* (A, F, MO), *Davidson 1056* (A, F, US). Llanos near El Hato del Volcán on road to Cerro Punta, 6000 ft, *Luteyn 3050* (DUKE, MO). Premontane cloud forest along ridge E of Cerro Horqueta, 1700–1900 m, *Luteyn & Wilbur 4602* (DUKE). Trail to summit, W slopes of Volcán de Chiriquí, 2500–3400 m, *Mori & Kallunki 5743* (DUKE, MO). N of San Félix at Chiriquí-Bocas del Toro border on Cerro Colorado copper mine road along continental divide, 5000–5500 ft, *Mori & Kallunki 5808* (DUKE, MO). Potrero Camp, Chiriquí Volcano, 2800–3000 m, *Pittier 3077* (F, US). Near peak, Volcán de Chiriquí, 11900 ft, *Terry 1316* (F), *1332* (A, F). W slope of El Barú above 10000 ft, *Tyson & Loftin 6133, 6138, 6155* (all DUKE). Valley of the upper Rio Chiriquí Viejo, *White 16* (MO). Slopes of Volcán Chiriquí, 9800 ft, *Wilbur et al. 11027* (DUKE, MO). Upper end of lava field NE of El Hato del Volcán, 6200 ft, *Wilbur et al. 17218* (DUKE). Finca Lerida, 1750 m, *Woodson & Schery 229* (GH, MO, NY). Casita Alta to Cerro Copete, 2300–3300 m, *Woodson & Schery 372* (GH, MO, NY). Potrero Muleto to Summit, Volcán de Chiriquí, 3500–4000 m, *Woodson & Schery 388* (GH, MO, NY); *Woodson & Schery 435* (GH, MO, NY). Casita Alta, Volcán de Chiriquí, 1500–2000 m, *Woodson et al. 813* (A, NA, NY). Loma Larga to summit, Volcán de Chiriquí, 2500–3380 m, *Woodson et al. 1050* (A, MO, NA, NY), *1071* (A, NA, NY), *1092* (MO).

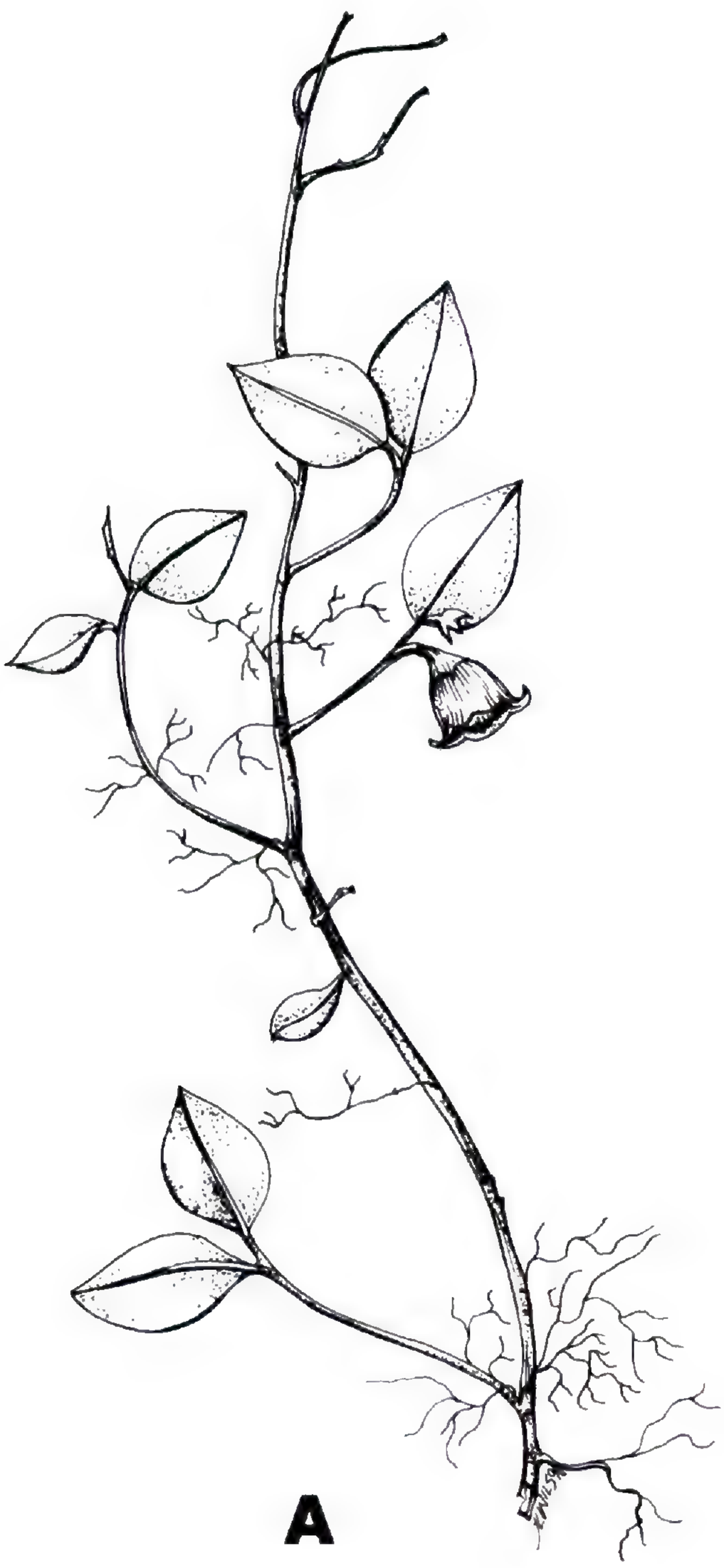
2. **Vaccinium dissimile** Blake, J. Bot. 53: 271. 1915. TYPE: Costa Rica: Prov. de San José; La Palma, 1550 m, *Tonduz* (C.R. Nat. Herb. *#12546*) *J. Donnell Smith 7380* (BM and K, syntypes neither seen; US, isotype).—FIG. 19.

Disterigma dissimile (Blake) Blake, Proc. Biol. Soc. Wash. 35: 120. 1922.

Creeping, epiphytic, viney *shrublets* with stems interwoven amongst the epiphytic bryophytes; stems wiry, perhaps to a meter long, 1–1.5 mm in diameter, the young stems densely spreading puberulent, glabrous in age. *Leaves* ovate, lance ovate or narrowly to broadly elliptic, coriaceous, entire, revolute, mostly 1.5–3.0(–4.0) cm long, 8–15(–18) mm wide, glabrous above and beneath or beneath sparingly to moderately beset with dark glandular, appressed trichomes 0.1–0.2 mm long, apically acute and basally rounded to cuneate; petioles 1–2 mm long, puberulent. *Inflorescences* of axillary, solitary flowers, pedicels 1–1.5 (–4 or fide A. C. Smith to 8) mm long, the bracteoles basal, 2, ovate to broadly oblong, opposite, obtuse to broadly rounded, puberulent, 0.8–1 mm long and nearly as wide. *Flowers* with the hypanthium campanulate, 2.2–2.8 mm long, densely hirsutulous with hyaline trichomes 0.1–0.2 mm long, the calyx lobes 4, broadly deltoid, acute, 0.7–0.8 mm long, moderately to densely hirsutulous; corolla red, campanulate, sparingly and inconspicuously beset with spreading, gland-tipped trichomes 0.1–0.2 mm long, the tube 7–9 mm long, 6–7 mm in diameter at the apex or the broadest point, the lobes 4, acutely deltoid, 1.5–2 mm long, erect; stamens 8, the filaments 3.5–4.0 mm long, sparsely pilose, elliptical, tapering both to the base and the apex where about 0.5 mm wide, the anthers medifixed, spurless, 2–2.5 mm long, conspicuously papillose granular, each sac tapering into an erect tubule 2–2.5 mm long which opens by an introrse cleft 0.5–0.7 mm long; ovary 4-loculate. *Berry* not seen.

This species is known from the cloud forests of parts of Costa Rica, Panama, and northwestern Colombia, but the plant is easily overlooked. Blake placed this species in the genus *Disterigma*, but Smith (1933) disagreed since the "pedicellary bracts, which are much smaller than those of typical species [of *Disterigma*], do not clasp the tube," "the pedicels themselves are usually longer than those described by Blake (up to 8 mm long), and the plant does not have the compact close-leaved habit of *Disterigma*." Sleumer (1936) established the monotypic section *Pseudodisterigma* Sleumer of *Vaccinium* for this species. It seemingly rests comfortably in neither genus but its proper placement must await generic reappraisal of the vaccinioid ericads.

BOCAS DEL TORO: Between Q. Gutierrez and E slope of La Zorra, headwaters of Río Mali, Chiriquí Trail, *Kirkbride & Duke 729* (MO). CHIRIQUÍ: Cloud forest, Cerro Colorado, 50 km N of San Félix, ca. 1400 m, *Dressler 5086* (DUKE, MO). COCLÉ: Cerro Pajita, hills N of El Valle 1100 m, *Allen 3782* (MO). La Mesa above El Valle, 800 m, *Croat 25431* (MO). Summit of Cerro Pilón above El Valle de Antón, ca. 2700 ft, *Dwyer 4488* (MO). La Mesa, 5 mi N of El Valle, 2500 ft, *Tyson et al. 2443* (DUKE). PANAMÁ: Premontane rain forest, Cerro Jefe, along trail on ridge running NE from summit, 1000 m, *Mori et al. 3756* (MO). Cerro Jefe, new road leading N from summit, *Witherspoon 8526* (DUKE, MO). VERAGUAS: Tropical wet forest, Atlantic slope, 11 km from Escuela Agrícola Alto de Piedra along Río Dos Bocas, *Mori & Kallunki 3177* (MO). NW of Santa Fé, 8.8 km from Escuela Agrícola Alto de Piedra, Pacific slopes, *Mori & Kallunki 3939* (MO).



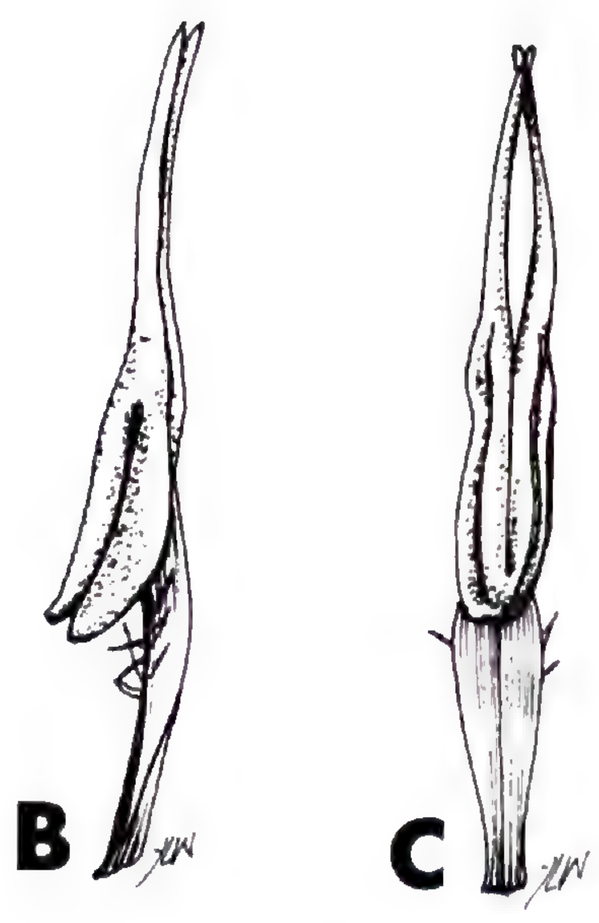


FIGURE 19. *Vaccinium dissimile* Blake.—A. Habit (×1).—B–C. Stamens.—B. Lateral view (×8¼).—C. Ventral view (×8¼). After *Wilbur 16898* (DUKE).]

3. **Vaccinium floccosum** (L.O. Wms.) Wilbur & Luteyn, Brittonia 29: 272. 1977.

Hornemannia floccosa L.O. Williams, Brittonia 18: 248. 1966. TYPE: Panama, *Davidson 104* (F, holotype; A, MO, US, isotypes).
Symphysia floccosa (L.O. Wms.) L.O. Wms., Phytologia 24: 158. 1972.

Terrestrial or epiphytic *shrub* 1–4 m tall with slender, grayish to olive brown, glabrous branchlets. *Leaves* indistinctly 3–5-plinerved and also somewhat arcuately veined, coriaceous, glabrous to moderately appressed glandular strigillose above and especially beneath, entire, slightly thickened at the margin, ovate to lanceolate or elliptic, apically acute to acuminate, basally cuneate to rounded, (3–)5–9(–11) cm long, (1.5–)3–5(–6.5) cm wide; petioles 2–4(–6) mm long, glabrous. *Inflorescences* axillary, umbelliform racemes mostly 2–4 cm long; peduncle glabrous to sparingly puberulent, 2–10 mm long; rachis glabrous to sparingly puberulent, 0.5–1 cm long; bracts persistent, ovate to lance ovate or lanceolate, glabrous to sparingly short ciliate, bracts 1–3 mm long basal; pedicels glabrous to sparsely puberulous, 1–2(–2.5) cm long; bractlets 2, to almost medial subopposite, ovate to lance ovate, persistent, glabrous to inconspicuously ciliate, 1–1.5 mm long. *Flowers* with the hypanthium campanulate, 2–3 mm high, 3–5 mm in diameter, glabrous, clearly disarticulating from the pedicel by a sharply delineated groove often fringed with glandular trichomes 0.1–0.2 mm long; calyx limb 0.8–1 mm tall, the lobes 5, broadly triangular, 2–3.5 mm long, acute, glabrous; corolla broadly cylindric, 0.7–1.0 cm long, 4–5 mm in diameter, externally glabrous to moderately appressed spiculate, internally densely floccose with a tangle of white, villous trichomes, pale greenish often suffused with red, the lobes 5, triangular, 2.0–2.2 mm long, apically acute, erect to spreading or even reflexed, densely villous floccose within; stamens 10, the filaments flattened, slightly adherent to the very base of the corolla tube, slightly ciliate, the anther sacs golden, attached on the lower ⅓, granular, basally inwardly curved, ca. 2.2 mm long, lacking horns and spurs, the tubules inconspicuous, stout ca. 1 mm long each with a terminal pore; style elevated upon a 1.2–1.5 mm long, granular, columnar projection from ovary. *Berries* succulent, dark purplish at maturity, 8–10 mm in diameter.

This species is endemic to the Chiriquí region of western Panama. Its synonymy listed above indicates something of its anomalous characteristics. The relationships of this species are as close to the species centered about *Vaccinium poasanum* as they are to the largely West Indian species usually treated as *Symphysia racemosa* (Vahl) Stearn (= *Hornemannia racemosa* Vahl). The inclusion of all these species within *Vaccinium* does not expand the limits of that extremely diverse genus.

CHIRIQUÍ: Cloud forest at Monte Rey near Boquete, *Croat 15856* (DUKE). Rain forest, Bajo Chorro near Boquete, 6000 ft, *Davidson 104* (A, F, MO, US), *423* (F). Cloud forest, Cerro Horqueta, 5800 ft, *Lewis et al. 552* (MO). Bajo Mono and Bajo Chorro trails out of Boquete, *Luteyn 3069* (DUKE, MO, NY). Bajo Mono trail NW of San Ramón towards headwaters of the Río Caldera, 1600–1700 m, *Luteyn 3728* (DUKE, MO, NY). Heavily forested slopes along a ridge of the western side of Cerro Horqueta, 1700–1800 m, *Luteyn 3756* (DUKE, MO, NY). Premontane cloud forest along ridge E of Cerro Horqueta, 1700–1900 m, *Luteyn & Wilbur 4600* (DUKE, MO, NY). Slopes approaching Cerro Horqueta, 1500–1800

m, 6.6 km NNE of Boquete, *Wilbur & Luteyn 19229* (DUKE, MO), *19251* (DUKE), *19330* (DUKE, F, GH, LL, MICH, MO, PMA, NY, US).

4. **Vaccinium jefense** Luteyn & Wilbur, Brittonia 29: 272. 1977. TYPE: Panama, *Luteyn & Kennedy 3955* (DUKE, holotype; MO, NY, isotypes).

Viney *epiphyte* or arching terrestrial *shrub* to 2 m tall; mature stems green becoming reddish brown, drying brown, subterete, glabrous; bark thin, cracking into longitudinal strips; immature branches and twigs of the new growth subterete, glabrous to densely hirsute distally. *Leaves* coriaceous, entire, elliptic or ovate elliptic, (4.5–)8–12(–13.5) cm long, (2.5–)3–7 cm wide, basally rounded and cordate, apically acuminate, dark green above and paler beneath, drying olive to grayish brown, glabrous above, sparsely to moderately hirsute beneath along the principal veins, the lower surface also with numerous minute glandular fimbriae; pinnately veined with 3 pairs of lateral nerves, the veins impressed above and raised beneath causing the leaves to be bullate, proximal 1–2 cm of midrib conspicuously thickened above; pseudostipules (bud scales) lanceolate, subulate, ca. 3 mm long, hirsute; petioles terete, rugose, hirsute, becoming glabrous, 5–9 mm long, 2–2.5 mm in diameter. *Inflorescence* axillary but often appearing terminal, racemose or subcorymbose, 8–17-flowered, the rachis, the pedicels, the bracteoles, the calyx and the corolla totally green; rachis 1–1.5 cm long, subterete, reddish brown, glabrous or sparsely hirsute, densely glandular fimbriate; floral bracts linear lanceolate, 3–9 mm long, ca. 1 mm wide, hirsute, glandular fimbriate, conspicuously nerved; pedicels terete, striate, sparsely hirsute, densely glandular fimbriate, ca. 15 mm long, 1 mm in diameter, elongating to 26 mm after anthesis, articulate with the calyx; bracteoles linear lanceolate, 5–8 mm long, ca. 0.5 mm wide, hirsute, glandular fimbriate. *Flowers* with the hypanthium and free portion of the calyx 7–9 mm long, sparsely to moderately hirsute and glandular fimbriate, the hypanthium cylindric, 10-ribbed, slightly angled opposite the sinuses, 2–2.5 mm long 2–3 mm in diameter; calyx limb campanulate, 5.5–7 mm long including the lobes, the lobes oblong or ovate, acute, often basally slightly imbricate, 5–6 mm long, 1.7–3 mm wide, conspicuously nerved; corolla cylindric, sparsely hirsute and glandular fimbriate especially on the surface of the lobes, 11–12 mm long, 5.5–7.5 mm in diameter, the corolla lobes triangular, ca. 3 mm long, basally ca. 3 mm wide; stamens 10, ca. 8 mm long, the filaments distinct, ca. 3 mm long, broadest basally, marginally densely sericeous especially on the connective, translucent when fresh, the anthers ca. 7 mm long, strongly curved inwards at the base, the thecae granular, ca. 3 mm long, orangish brown when fresh, the tubules ca. 4 mm long, sparsely pilose, dehiscing by laterally oriented apical slits ca. 1.5 mm long, yellowish brown; style included, glabrous, 9–10 mm long.

Vaccinium jefense resembles *V. floccosum* (Panama), *V. poasanum* (Guatemala-Panama), *V. costaricense* Wilbur & Luteyn and *V. orosiense* Wilbur & Luteyn (both endemic to Costa Rica) in having short racemose, umbellate to subcorymbose inflorescences with green or yellowish corollas; however, it differs most significantly in its pinnately veined leaves, glandular inflorescence, elongate bracteoles, and anther tubules dehiscing by latrorse clefts. This lateral

dehiscence seems to be exceptional in the genus. From *V. floccosum*, *V. costaricense* and *V. orosiense*, the new species further differs in its longer calyx lobes, internally glabrous corolla and anther tubules nearly twice as long.

PANAMÁ: 1 milla depués de La Eneida cerca de Cerro Jefe, 750 m, *Correa & Dressler* 955 (DUKE, MO, PMA). La Eneida near Cerro Jefe, *Dressler 3541* (MO, PMA). Path beyond the village of La Eneida, 1000 m, *Luteyn & Foster 1124* (DUKE, F, MO, US). Top of Cerro Jefe, 1000 m, *Luteyn & Kennedy 3955* (DUKE, MO, NY). Altos de Pacora, 15–20 km WNW of Cerro Azul, premontane rain forest, 800 m, *Mori 6910* (DUKE). NE from summit of Cerro Jefe, 1000 m, *Mori & Kallunki 6080* (DUKE). Altos de Pacora, 15–20 km WNW of Cerro Azul, 800 m, *Mori et al. 6910* (MO). Cloud forest on Cerro Jefe, 1000 m, *Mori 7110* (MO). Top of Cerro Jefe, *Tyson et al. 4344* (DUKE, MO, SCZ). New road leading N from summit of Cerro Jefe, *Witherspoon 8558* (DUKE, MO).

5. **Vaccinium poasanum** Donnell Smith, Bot. Gaz. (Crawfordsville) 24: 395. 1897. LECTOTYPE: Costa Rica, *J. Donnell Smith 6634* (US).

Epiphytic or terrestrial *shrubs* or small *trees* (1–)2–5(–10?) m tall with glabrous branchlets and branches. *Leaves* indistinctly 3–5-plinerved and also somewhat arcuately veined, coriaceous, glabrous or sparingly to moderately appressed glandular strigose above and especially beneath, rarely short puberulent near the base, entire, slightly revolute, ovate to lanceolate or elliptic, acute to acuminate, 3–8(–10) cm long, (1–)2.5–4(–6) cm wide; petioles 1–4 mm long, glabrous to hirsutulous. *Inflorescences* axillary, umbelliform racemes mostly 2–4 cm long; rachis glabrous to sparingly puberulent, 0.5–2 cm long; bracts persistent, lance ovate to lanceolate, ciliate, 1.5–2.5 mm long; pedicels slender, sparingly puberulent, 7–15 mm long in flower, the bractlets 2, submedial, subopposite, lance ovate to lanceolate, often persistent, ciliate, 1–1.5 mm long. *Flowers* with the hypanthium short campanulate to turbinate, 2–3.5 mm high and about equal in diameter, glabrous to densely puberulent, clearly disarticulating from the pedicel by a marked groove and often with a fringe of glandular trichomes 0.1–0.2 mm long; calyx limb 0.5–0.7 mm tall, the lobes 5, broadly and shallowly deltoid with an apiculate tip 0.2–0.5 mm long; corolla broadly cylindric, 8–12 mm long, 6–10 mm in diameter, externally and internally glabrous or apically sparsely, villose, pale yellowish or greenish white and occasionally tinged with bright rose or pink, the lobes 5, broadly oblong, 2–3.5 mm long, apically acute to obtuse, erect to slightly recurved; stamens 10, the filaments 2–2.5 mm long, ciliate, flattened, broadened basally where slightly adherent to the very base of the corolla tube, the thecae golden, attached slightly above the middle, granular, basally inwardly curved, 1.8–2.2 mm long, lacking horns or spurs but with slender yellowish tubules 3.5–5.5 mm long each with a slightly inwardly oblique pore; style greenish, 8–10 mm long. *Berries* succulent, yellowish but turning dark purple at maturity, subglobose, 7–10 mm in diameter.

This species is known from the mountains of Guatemala, Honduras, El Salvador, Costa Rica and western Panama and throughout much of its range it is abundant and often conspicuous.

CHIRIQUÍ: Las Nubes, 5.5 km NW of Río Chiriquí Viejo, W of Cerro Punta, 2200 m, *Busey 665* (DUKE). Rain forest, Bajo Chorro, 6000 ft, *Davidson 311* (A, F, US), *353* (A, F, MO, US). Premontane cloud forest along ridge E of Cerro Horqueta, 1700–1900 m, *Luteyn*

& Wilbur 4599 (DUKE, MO); *Luteyn & Wilbur 4622* (DUKE). Cerro Pando on the continental divide and the Panama-Costa Rica border, 16 km NW of El Hato del Volcán, 2000–2482 m, *Mori & Bolten 7332* (MO). Cerro Colorado 50 km N of San Félix on the continental divide, cloud forest, 1200–1500 m, *Mori & Dressler 7777* (MO). Lower montane rain forest N of San Félix at Chiriquí Bocas del Toro border on Cerro Colorado copper mine road along continental divide, 5000–5500 ft, *Mori & Kallunki 5890* (DUKE, MO). San Ramón near Bajo Mono 4 mi NW of Boquete, 6000 ft, *Wilbur et al. 13528* (DUKE, MO, PMA). E of Guadeloupe along the Río Chiriquí Viejo, 2 mi NE of Cerro Punta, 7000 ft, *Wilbur & Foster 13114* (DUKE, MO, PMA). 6.6 km NNE of Boquete, *Wilbur & Luteyn 19226* (DUKE, MO). Cerro Punta beyond Las Nubes, 7500 ft, *Wilbur & Teeri 13205* (DUKE).

6. **Vaccinium santafeënsis** Wilbur & Luteyn.[7] TYPE: Panama, *Mori & Kallunki 5248* (MO, holotype).

Epiphytic *shrub* to 3 m tall, vegetatively glabrous throughout; mature stems and twigs terete, gray to light brown when dry. *Leaves* elliptic, drying subcoriaceous, 5–8 cm long, 2–3 cm wide, basally cuneate, apically acute, acuminate or tapering into a pronounced drip-tip 8–12 mm long, the venation pinnate, the midvein elevated proximally above sunken distally, elevated throughout beneath; petioles dorsiventrally compressed, 6–11 mm long, 1.5–2.0 mm wide. *Inflorescences* short racemose or subcorymbose, 2–8-flowered; rachis terete, smooth or weakly striate, 5–9 mm long; pedicels terete, smooth to finely striate, 8–12 mm long at anthesis; floral bracts ovate to oblong ovate, keeled, acute, irregularly and minutely marginally fimbriate, 1.0–1.2 mm long, appressed; bracteoles slightly smaller and more closely appressed, ca. 1 mm long, minutely fimbriate. *Flowers* with the hypanthium ca. 2 mm long, terete, ca. 2.5 mm in diameter, sharply articulate with the pedicel, the disarticulating groove marked by fimbriae; calyx limb shallowly campanulate to flaring, ca. 1 mm long, the lobes 5, ca. 0.6 mm long, broadly triangular, the sinuses shallowly indented to almost flat; corolla cylindric, abruptly contracted for the lower 1.5–2 mm where 2.2–2.5 mm in diameter, 4.0–4.2 mm in diameter above, 8–9 mm long, "light pink," the lobes 5, triangular, acute, erect, 2.0–2.5 mm long; stamens 10, 6–7 mm long, the filaments distinct or weakly coherent basally, flattened, 2.0–2.2 mm long, ca. 0.5 mm wide, distally ciliate, the anther sacs medifixed, 2.0–2.5 mm long, coarsely granular, the 2 distinct tubules 3.0–3.2 mm long, dehiscing by elongate, lateral clefts 2.0–2.5 mm long; style exserted, 9–10 mm long. Mature *berry* not seen.

VERAGUAS: Cloud forest on ridge top below summit of Cerro Tute, NW of Santa Fé, 2 km from Escuela Agrícola Alto de Piedra, *Mori & Kallunki 5249, 5280* (both MO).

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[7] *Vaccinium santafeensis* Wilbur & Luteyn, sp. nov. Frutex epiphyticus ca. 3 m altus. Folia subcoriacea, elliptica, pinnatinervia, 5–8 cm longa et 2–3 cm lata. Inflorescentia axillaris, racemosa vel subcorymbosa; flores 2–8; pedicelli articulati 8–12 mm longi; bracteae et bracteolae ovatae vel oblong-ovatae fimbriatae 1–1.2 mm longae. Hypanthium ca. 2 mm longum; limbo campanulato ca. 1 mm longo; lobis ca. 0.6 mm longis. Corolla cylindrica glabra 8–9 mm longa; lobis triangular-acutis erectis 2–2.5 mm longis. Stamina ca. 6–7 mm longa; filamenta distincta 2–2.2 mm longa ciliata; thecis 2–2.5 mm longis, granularibus basi introsum curvis; tubulis anthearum 2 ad basim distinctis 3–3.2 mm longis; rimis elongatis lateralibus, 2.0–2.5 mm longis.

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FLORA OF PANAMA[1]

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part VIII

FAMILY 155. EBENACEAE

F. WHITE[2]

Trees, *shrubs* or rarely suffruticose from a woody rhizome, without milky sap; heartwood sometimes black; indumentum usually of simple, unicellular, setose, strigose, or sericeous hairs, but multicellular glandular, unicellular bibrachiate, and multicellular peltate hairs sometimes present. *Leaves* usually alternate, rarely opposite, exstipulate, entire, the epidermal cells papillose in some species, mostly in those with a glaucous lower epidermis. *Flowers* actinomorphic, hypogynous, unisexual, but often with well-developed staminodes or pistillodes, solitary, fasciculate, cymose or rarely in false racemes or panicles; calyx gamosepalous, entire to deeply lobed, sometimes closed in bud, otherwise with open or imbricate aestivation, always persistent in fruit and often accrescent; corolla gamopetalous with contorted aestivation, shortly to deeply lobed, rotate, urceolate, salver-shaped or sausage shaped, often constricted at the throat; stamens 2–100+, epipetalous or borne on the receptacle, the filaments usually short and flattened, the anthers lanceolate or sagittate, often 2 or more arising from a single filament, usually dehiscing by lateral slits, rarely by apical pores, the connective well developed, often larger than the anthers, often apiculate or rostrate; ovary syncarpous, 2–5 or more carpellary, the carpels 2-ovulate, usually completely or partly divided by a false septum, rarely unilocular, the ovules pendulous from the apex of the locule, the styles distinct or basally connate, less often more or less completely united, the stigmas usually large, fleshy and irregularly lobed. *Fruit* a berry, rarely tardily dehiscent; seeds large; endosperm abundant, hard, sometimes ruminate; embryo relatively small, straight or slightly curved, the radicle well developed, the cotyledons flat, oval, foliaceous, usually emergent, either persistent and photosynthetic or fugaceous and non photosynthetic.

The Ebenaceae is a family with 2 genera; *Euclea* Murr. with a dozen species is confined to Africa, and the pantropical *Diospyros* has ca. 80 species in America, 94 on the African mainland, ca. 100 in Madagascar, and ca. 200 in tropical Asia and the Pacific. It shows only feeble penetrations into temperate latitudes and is poorly represented on tropical mountains.

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[1] Assisted by National Science Foundation Grant DEB 77-04300 (W. G. D'Arcy, principal investigator).

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ANN. MISSOURI BOT. GARD. 65: 145–154. 1978.

0026-6493/78/0145–0154/$01.15/0

Among Panamanian families the Ebenaceae appears to be most closely related to the Sapotaceae, from which it differs *inter alia* in the articulated, unisexual flowers, biovulate carpels with apical placentation, bitegmic ovules, the small hilum of the seed, and the absence of latex.

The number of floral parts in Ebenaceae is very variable, both between and within species. The unripe fruit is very astringent but the ripe fruit of most species is edible, though in a few species it is used as a fish poison. The whole fruit is usually the unit of dispersal but it seems that in *D. salicifolia* individual seeds with adherent pericarp are removed by birds or small mammals while the fruit is still attached to the tree.

The Central American species *D. digyna* has been planted in many parts of the tropics for its edible fruit. *Diospyros blancoi* A. DC., a native of the Philippines which also has an edible fruit has been planted in a few places in Panama. It is much better known under the illegitimate name *D. discolor* Willd.

Our knowledge of Panamanian Ebenaceae is very incomplete and more collecting is needed. No species is represented in herbaria by complete material. In this account 4 species are provisionally given specific names. All four are widespread and variable, and the Panamanian representatives are somewhat different from their relatives elsewhere. Further work may lead to the recognition of distinct subspecies. The descriptions of the flowers of *D. digyna*, *D. salicifolia*, and *D. artanthifolia* (in part) are based on non-Panamanian material.

Literature:

Hiern, W. P. 1873. A monograph of Ebenaceae. Trans. Cambridge Philos. Soc. 12: 27–300.

Howard, R. A. 1961. The correct names for "*Diospyros ebenaster*." J. Arnold Arb. 42: 430–435.

1. DIOSPYROS

Diospyros L., Sp. Pl. 1057. 1753. TYPE: *D. lotus* L.

Characters as given for family.

KEY TO FRUITING SPECIMENS

a. Fruits borne in a lax, richly branched infructescence; calyx 0.5 cm long with (4–) 5(–6) acute, deltate teeth ..... 1. *D. artanthifolia*
aa. Fruits solitary or in 2–3-flowered fascicles.
  b. Calyx cup-shaped; leaves to 9 cm long and 4 cm wide ..... 4. *D. salicifolia*
  bb. Calyx saucer-shaped; leaves much larger.
    c. Fruits distinctly pedicellate, at least 2.5 cm in diameter.
      d. Fruits ca. 2.5 cm in diameter; calyx lobed to the middle . 3. *D. inconstans*
      dd. Fruits at least 4 cm in diameter; calyx shallowly lobed ..... 2. *D. digyna*
    cc. Fruits subsessile, to 1.5 cm in diameter ..... 5. *D.* sp. I

KEY TO FLOWERING SPECIMENS[3]

a. Corolla lobes 4–5.
  b. Corolla lobes much longer than the tube ..... 1. *D. artanthifolia*

[3] The flowers of *D.* sp. I. are unknown.

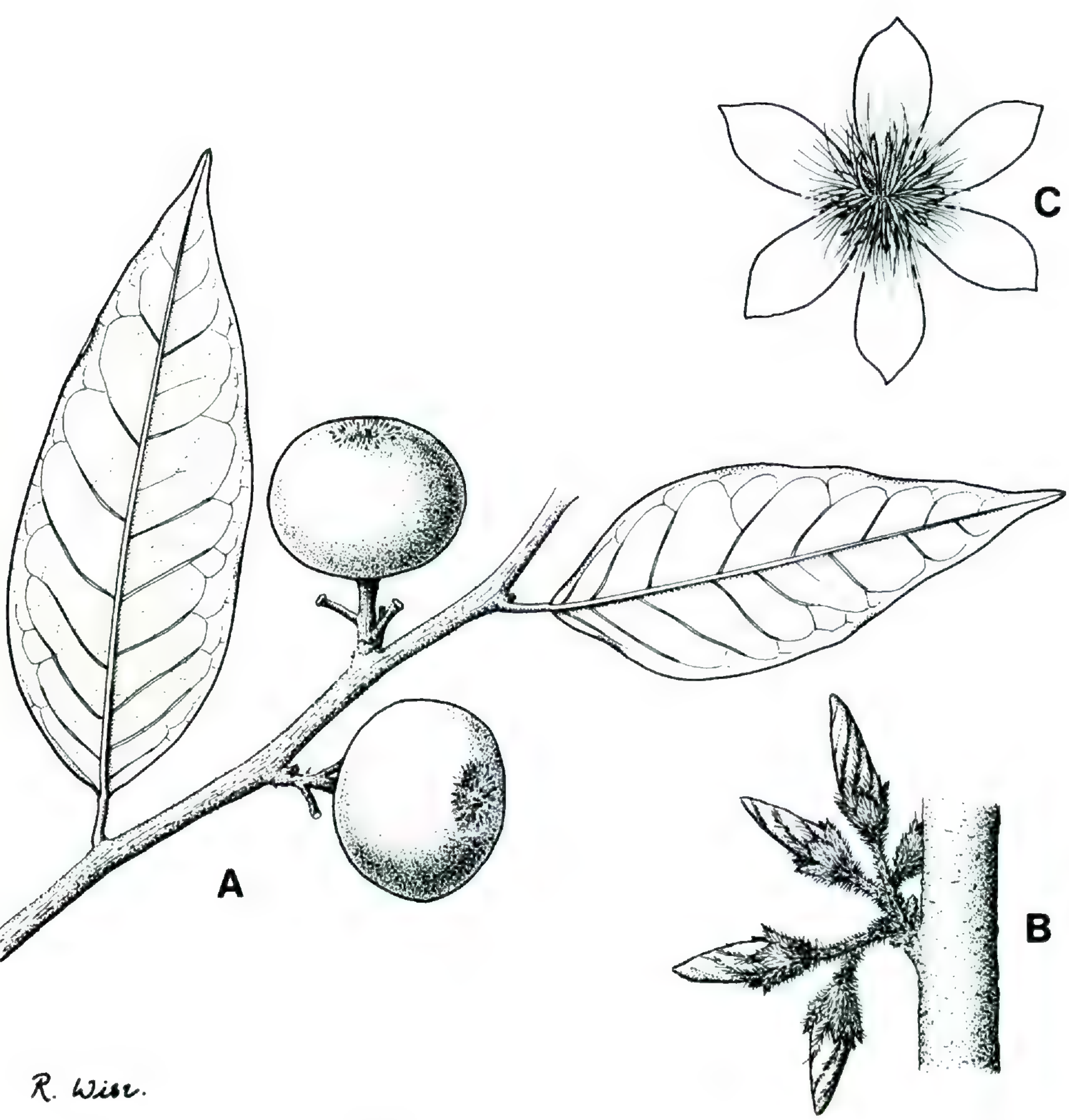

FIGURE 1. *Diospyros artanthifolia* Mart.—A. Leaves and fruits (×7/10). [After *Nee 7862* (MO).]—B. Male inflorescence (×2⅕).—C. Male flower (×3). [After *Croat 14657* (MO).]

bb. Corolla lobes much shorter than the tube ..... 2. *D. digyna*
aa. Corolla lobes 3.
c. Leaves to 9 cm long and 4 cm wide, the tertiary nerves and veins indistinct ..... 4. *D. salicifolia*
cc. Leaves much larger, the tertiary nerves and veins forming a close and conspicuous reticulum ..... 3. *D. inconstans*

1. **Diospyros artanthifolia** Mart., Fl. Bras. 7: 7. 1856. TYPE: Maynas, Peru, *Poeppig 2266* (BR, holotype; L, OXF, W, isotypes; FHO, US, photos).—FIG. 1.

Tree 4–15 m tall; branches long, slender, subverticillate; branchlets setulose-tomentellous. *Leaves* chartaceous, drying brownish black above, paler brown beneath; lamina to 11 cm long and 4 cm wide, lanceolate, broadest just above

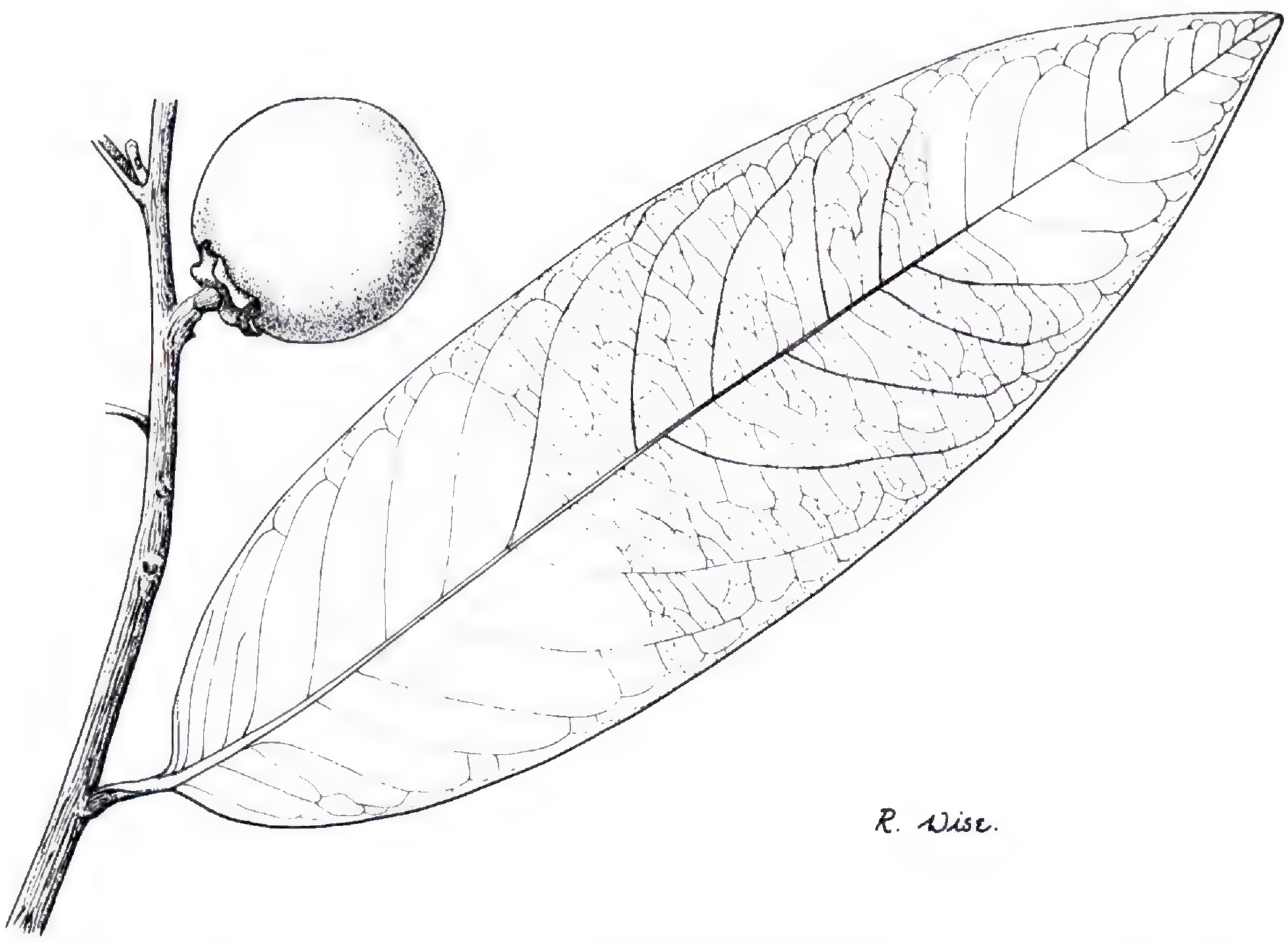

FIGURE 2. *Diospyros digyna* Jacq. Leaf and fruit (×⅗). [After *Gentry* 6227 (MO).]

the base, the apex acuminate, the base cuneate, the margin revolute, the lower surface strigose-puberulous and rough to the touch, the lateral nerves in 7–10 pairs, slightly impressed above, prominent beneath, the intercostal and other nerves forming a subprominent lax reticulum beneath. *Male flowers* in 7–25-flowered axillary cymes; pedicels 0.1–0.4 cm long; calyx 0.3–0.4 cm long, densely strigillose outside, sparsely strigillose inside, the lobes (4–)5(–6), deltate, about as long as the tube; corolla ca. 0.6 cm long, fusiform in bud, subrotate at anthesis, glabrous outside except for the densely strigose mid-petaline lines, the tube 0.2 cm long, obconic, the lobes 5, lingulate; stamens ca. 30, 0.25–0.35 cm long, attached to the base of the corolla tube, exserted, the connective with long setae to 0.3 cm long; pistillode absent. *Female flowers* in ca. 5-flowered axillary cymes, pedicels to 0.5 cm long; calyx and corolla similar to those in male flowers but larger; staminodes ca. 6; ovary 0.4 cm long, 0.4 cm wide, ovoid-conoidal, the styles 4–5, 0.4 cm long, divergent, united only at the base, locules 8 or 10, uniovular. *Fruit* ca. 4 cm in diameter, subglobose, hispidulous; seeds 8 or 10 or fewer by abortion, 2 cm long, 0.9 cm wide, 0.6 cm thick, black; endosperm smooth; fruiting calyx scarcely accrescent.

This species ranges from Panama southwards to Brasil.

CANAL ZONE: Barro Colorado Island, *Croat 14657* (MO). Piña, *Gentry 8724, 8731* (both FHO). Ten km NW of Gamboa, *Nee 7862* (FHO). DARIÉN: Santa Fé, *Duke 8403* (MO).

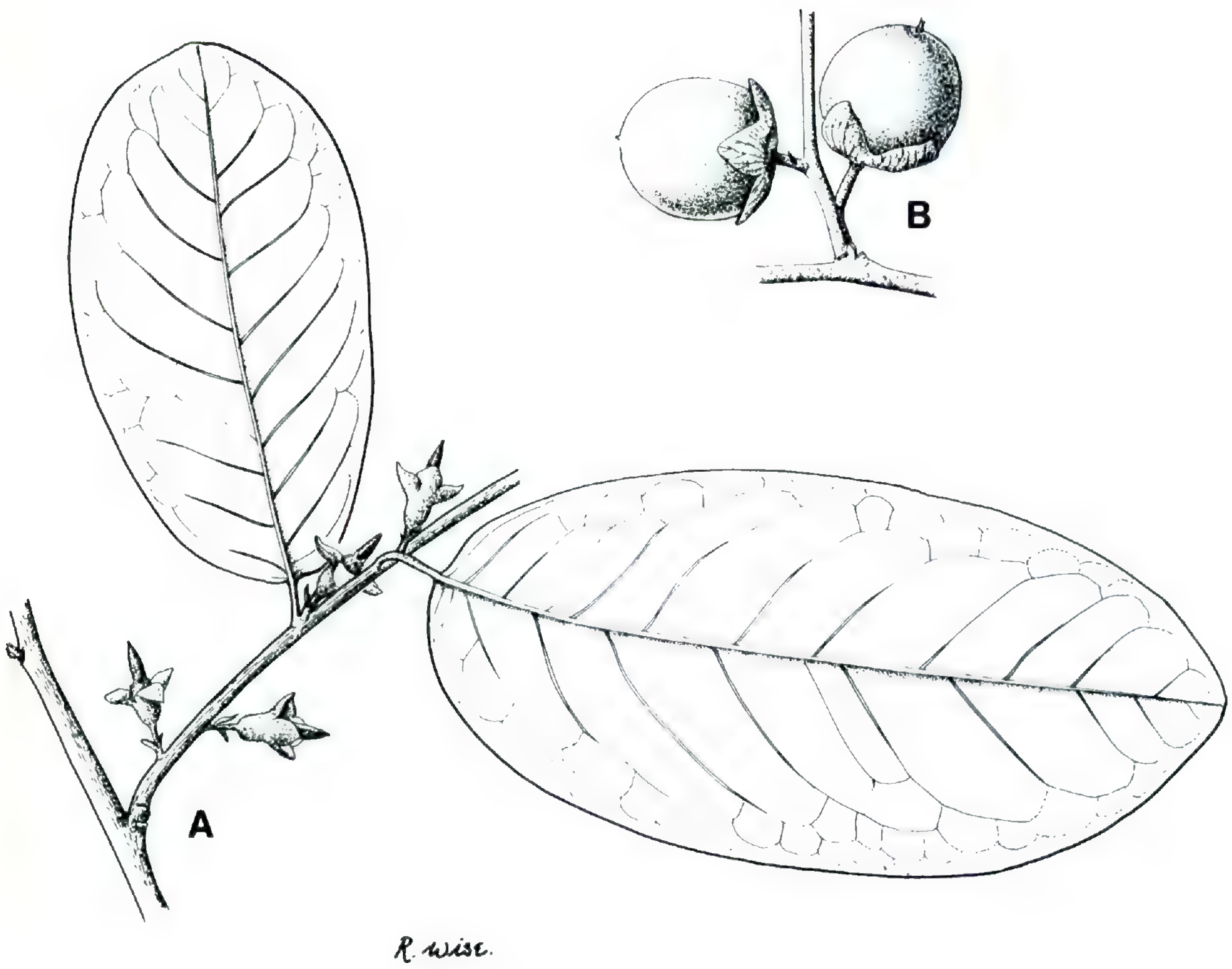

FIGURE 3. *Diospyros inconstans* Jacq.—A. Leaves and female flowers (×⅗). [After *Croat & Porter 15467* (MO).]—B. Fruit (×⅗). [After *Gentry 13458* (MO).]

2. **Diospyros digyna** Jacq., Hort. Schoenb. 3: 35, *tab. 313.* 1798. TYPE: Hort. Schoenb. 3: *tab. 313.* 1798.—FIG. 2.

Tree to 20 m tall; bark black, scaling in small pieces; branchlets minutely strigillose. *Leaves* subcoriaceous, drying grey green or blackish; lamina to 18 cm long and 7 cm wide, elliptic, oblong-elliptic or lanceolate-elliptic, the apex obtuse to subacuminate, the base cuneate, the lower surface glabrous except for a few minute, in part forking, strigillose hairs, the lateral nerves in 8–12 pairs, the tertiary and other veins forming a close but inconspicuous reticulum. *Male flowers* subsessile in ca. 5-flowered cymules in the axils of leaves or bracts towards the base of the current year's shoot; peduncle ca. 0.5 cm long; calyx to 1 cm long, minutely puberulous on both surfaces, the tube cup shaped, 0.4–0.5 cm long, the lobes 4–5, ca. 0.5 cm long, plicate, reduplicate; corolla to 1.8 cm long, more or less conical in bud, urceolate at anthesis, the tube ca. 1.2 cm long, strigillose-tomentellous outside, the lobes 4–5, suborbicular, 0.6 cm long, 0.6 cm wide, glabrous except for the sparsely strigillose part which is exposed before the flower opens; stamens ca. 20, to 0.9 cm long, attached mostly in pairs to the base of the corolla tube, included, the filament and connective densely strigillose, the connective short apiculate; ovary rudimentary, minute, setulose. *Female flowers* solitary or in fascicles of 2–3, borne otherwise as in the male

flowers; calyx and corolla similar to those in the male flowers but the calyx longer and the corolla shorter and broader; staminodes ca. 12, 0.3–0.8 cm long, attached to the base of the corolla tube; ovary 0.5 cm long, 0.4 cm wide, subglobose, tomentellous, the styles 4–5, ca. 0.5 cm long, united at the base, ending on the inner face in fleshy, irregularly lobed stigmas, the locules 8 or 10, uniovulate. *Fruit* (4–)6–8 cm in diameter, subglobose, black and glabrous when ripe; seeds 8 or 10 or fewer by abortion, 2 cm long, 1 cm wide, 0.5 cm thick, reddish brown; endosperm not ruminate; fruiting calyx 1.4–2 cm long, saucer shaped, glabrous outside, tomentellous inside, the lobes hemiorbicular to ovate, 0.6–0.9 cm long, the margin undulate.

Diospyros digyna, which has edible fruit, extends southwards from Mexico to Panama and Colombia. For centuries it has been extensively cultivated elsewhere in the tropics and is widely known under the name *Sapote negro*. Until recently its place of origin was uncertain. Because of its wide dissemination as a cultivated plant its nomenclatural history is complex, and for a long time it was known under erroneous or invalid names. Howard (1961) has recently established the correct name.

VERAGUAS: above Santa Fé on slopes of Cerro Tute below Agricultural School, *Gentry 6227* (FHO).

3. **Diospyros inconstans** Jacq., Enum. Pl. Carib. 34. 1760; Sel. Stirp. Amer. 276, *tab. 174, fig. 67*. 1763. TYPE: New Granada, Carthagena, *Jacquin* (not seen).—FIG. 3.

Small *tree* 5–8 m tall; branchlets sparsely and minutely strigillose. *Leaves* chartaceous, drying dull dark brown, paler beneath; lamina to 16 cm long and 7 cm wide, oblong-elliptic, the apex rounded to shortly cuspidate, the base rounded to obtuse, the lower surface sparsely and minutely setulose, the lateral nerves in 7–10 pairs, prominent beneath, paler than the lamina, the nerves and veins forming a close and conspicuous reticulum. *Male flowers* subsessile or shortly pedicellate in mostly 3-flowered, shortly pedunculate cymules; calyx to 0.7 cm long, strigillose-puberulous outside and inside, the lobes 3(4), imbricate, as long as the tube, suborbicular, apiculate; corolla ca. 1.5 cm long, subrotate, the tube ca. 1 cm long, densely strigose, lobes 3, 0.5 cm long, 0.45 cm wide, suborbicular-apiculate, glabrous except for the strigose mid-petaline lines; stamens ca. 10, to 0.4 cm long, attached to the base of the corolla tube, included, glabrous, the connective long-apiculate; pistillode absent. *Female flowers* solitary in the axils of leaves or of reduced leaves towards the base of the current year's growth; pedicel to 0.4 cm long; calyx 0.4 cm long, 0.5 cm wide, shallowly cup shaped, sparsely strigillose outside, tomentellous inside, the lobes 3, 0.2 cm long, rounded, the margin reflexed; corolla similar to that in male flower but shorter and broader; staminodes 3, attached to the base of the corolla tube; ovary 0.25 cm long, 0.25 cm wide, subglobose, strigillose-tomentellous, the style 0.15 cm long, stout, undivided, ending in 3, fleshy, bi-lobed stigmas, the locules 6, uniovulate. *Fruit* ca. 2.5 cm long, 2.5 cm wide, subglobose, glabrous; seeds 6, or fewer by abortion, 1.5 cm long, 0.8 cm wide, 0.5 cm thick, brownish

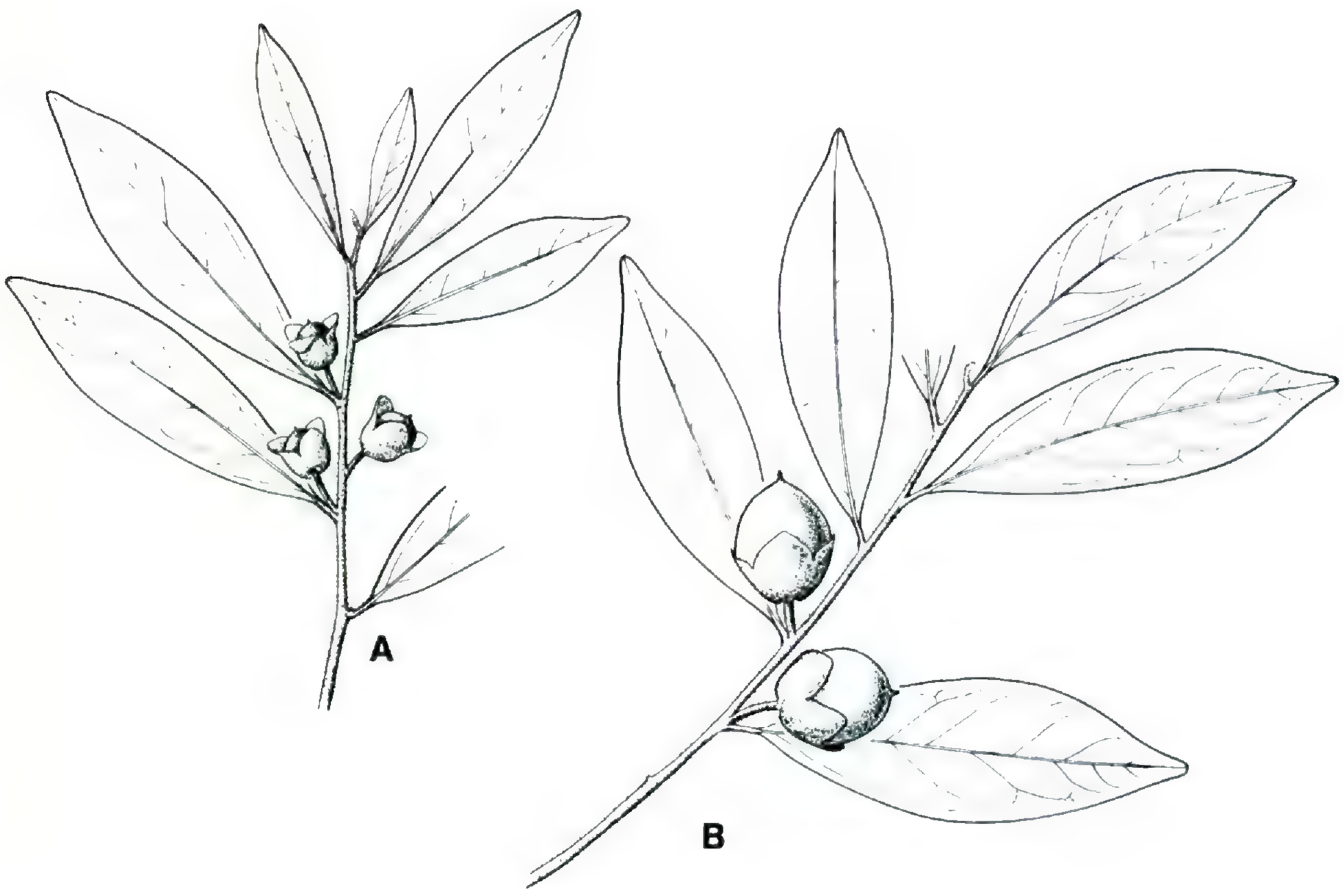

FIGURE 4. *Diospyros salicifolia* H. & B. ex Willd.—A. Leaves and young fruit (×⅗). [After *Dwyer & Hayden 7525* (MO).]—B. Leaves and mature fruit (×⅗). [After *Tyson 1819* (MO).]

black; endosperm smooth; fruiting calyx ca. 1.2 cm long, saucer shaped, lobed to the middle, sparsely puberulous outside, tomentellous inside.

Following Hiern (1873), this species is interpreted in a wide sense. It extends southwards from Panama and the West Indies to Paraguay and Argentina. Specimens from some parts of this enormous geographical range, especially from the extremities, are so different that it is difficult to believe that they belong to the same species. They are, however, connected by a complex series of intermediates.

DARIÉN: El Real, *Croat & Porter 15467* (MO). El Real, Quebrada Trapiche, *Duke 324* (MO). El Real, *Gentry 4508* (MO), *13458* (FHO). El Real, Río Tuira, *Stern et al. 455* (GH, UC, US), *763* (GH, MO, US).

4. **Diospyros salicifolia** Humb. & Bonpl. ex Willd. in L., Sp. Pl., ed. 4. 4: 112. 1805. TYPE: ? near Acapulco, Mexico, *Humboldt & Bonpland* (B, not seen; photo FHO).—FIG. 4.

Shrub or *tree* to 15 m tall; branchlets tomentellous with short hairs and longer sparser spreading hairs. *Leaves* chartaceous, drying reddish brown or yellowish brown; lamina to 9 cm long and 4 cm wide, oblanceolate, the apex

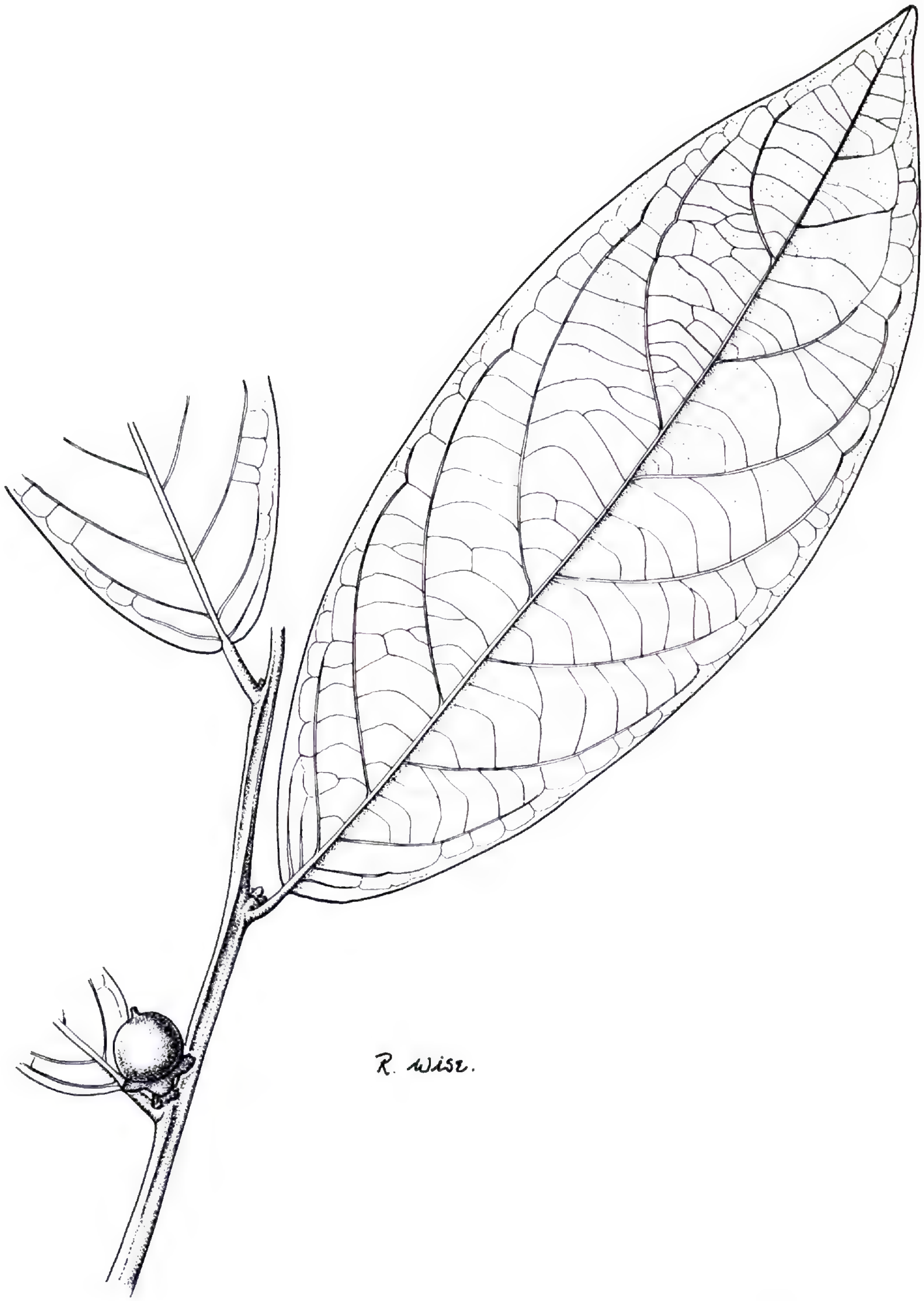

FIGURE 5. *Diospyros* sp. I. Leaf and fruit (×⅘). [After *Bristan 1229* (MO).]

acute to subacuminate, the base cuneate, the lower surface densely strigose on the midrib, more sparsely so elsewhere, the lateral nerves in 4–6 pairs, indistinct, the tertiary nerves and veins forming an indistinct reticulum. *Male flowers* subsessile in (1–)3(–5)-flowered, shortly pedunculate cymules; calyx to 0.6 cm long, tomentellous outside and inside, the lobes 3, with valvate or open deltate aestivation, as long as the tube; corolla ca. 1.2 cm long, narrowly urceolate, densely strigose outside except for the margins of the lobes, the lobes 3, deltate, 0.3 cm long, 0.15 cm wide; stamens ca. 9, to 0.5 cm long, attached to the base of corolla tube, included, glabrous, the connective long-apiculate; pistillode 0.1 cm long, 0.1 cm wide, densely setulose. *Female flowers* solitary, in the axils of leaves or of reduced leaves towards the base of current year's growth; pedicel 0.1–0.4 cm long; calyx similar to that in the male flower but to 0.9 cm long and the lobes valvate-reduplicate in young flower; corolla ca. 1.5 cm long, otherwise as in the male flower; staminodes 6, ca. 0.3 cm long, glabrous, attached to the corolla tube, 3 opposite to and 3 alternating with the lobes; ovary 0.3 cm long, 0.2 cm wide ovoid-conoidal, strigillose-tomentellous, the style 0.15 cm long, stout, undivided, ending in 3, fleshy, bi-lobed stigmas, the locules 6, uniovulate. *Fruit* ca. 3 cm long, 3 cm wide, orange yellow, glabrous, globose; seeds 6, or fewer by abortion, 1.4 cm long, 0.7 cm wide, 0.5 cm thick, reddish brown; endosperm smooth; fruiting calyx accrescent, to 1.5 cm long, cup shaped, shallowly lobed, sparsely puberulous outside, tomentellous inside.

Diospyros salicifolia is widely distributed in Central America from Mexico (Sinaloa) to Panama. It occurs in a wide range of forest types up to 1,000 m, varying from swamp forest to scrub forest on dry rocky slopes. The fruit frequently is not the unit of dispersal, but the seeds are often removed singly, possibly by birds, while the fruit is still on the tree.

CANAL ZONE: Farfan Beach, *Dwyer & Hayden 7525* (F, COL, MO, SCZ, UC); *Tyson 1819* (MO). DARIÉN: Cativo swamp, Río Chucanuque, about half an hour below Mortí, *Duke 11739a* (MO).

5. **Diospyros** sp. I.—Fig. 5.

Tree; branchlets irregularly compressed, sparsely and minutely strigillose. *Leaves* chartaceous, drying reddish brown; lamina to 20 cm long and 8 cm wide, more or less elliptic, the apex shortly subacuminate, the base rounded, slightly asymmetrical, the lower surface glabrous except for a few minute strigillose hairs, the lateral nerves in 6–8 pairs, prominent beneath, the tertiary nerves subscalariform. *Male flowers* unknown. *Female* flowers in axillary 2–3-flowered fascicles, otherwise unknown; pedicels (in fruit) ca. 0.2 cm long. *Fruit* subglobose, ca. 1.5 cm long and 1.5 cm wide, glabrescent with patches of persistent sericeous hairs; fruiting calyx 0.6 cm long, saucer shaped, sparsely strigillose outside, more densely so inside, 4-lobed, the lobes 0.3 cm long, hemiorbicular.

This species seems closely related to the Mexican and Guatamalan species *D. campechiana* Lundell.

DARIÉN: Cerro Pirre, *Bristan 1229* (FHO, MO).

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Numbers in **bold face** type refer to descriptions; numbers in roman type refer to synonyms; numbers with dagger (†) refer to names incidentally mentioned.

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FLORA OF PANAMA[1]

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part IX

FAMILY 177. ACANTHACEAE[2]

L. H. DURKEE[3]

Herbs, shrubs, vines or small *trees*. *Leaves* simple, opposite, exstipulate, often with cystoliths on the upper surface. *Flowers* irregular to nearly regular, perfect, borne in spikes, racemes, panicles, cymes or singly and often subtended by a conspicuous bract with 2 bracteoles; calyx synsepalous at least basally, persistent, the segments 5(4, 3); corolla gamopetalous, the limb 5-lobed or 2-lipped, rarely 1-lipped; stamens adnate to the corolla tube, 4 and didynamous or 2 only, the staminodes often present in flowers with 2 stamens, the anther cells 2 or 1, longitudinally dehiscent; ovary 2-celled, 2–10 ovules in each cell, the style filiform, simple, the stigmas 1 or 2. *Fruit* a capsule (except *Mendoncia* with drupaceous fruits), usually more or less stalked, 2-celled, 2-valved; seeds usually flattened, mostly borne on hook-shaped funicles, sometimes on papilliform funicles, the testa smooth or roughened, often mucilaginous when moistened.

The Acanthaceae includes about 250 genera and 2,500 species, mostly in the New and Old World tropics, with a few species extending into warm temperate regions. The family is divided into 4 subfamilies according to Lindau (1895). More recent considerations have restricted the genera to be included in the family (Bremekamp, 1953, 1965).

The Acanthaceae can be recognized by the prominent cystoliths appearing with magnification as small, cylindrical concretions or short lines on the upper surface of the leaves, the younger stems, the branches of the inflorescence, and the calyx. Genera lacking these are few and have exceptional features in the fruit. The genus *Mendoncia* is unique with a drupaceous fruit. The only genera lacking cystoliths and having the more typical capsular fruit with hooklike funicles are the genera *Aphelandra* and *Megaskepasma*. Seeds are frequently ejected forcefully by the hook-shaped funicle when the mature capsules are moistened by rainfall. In capsules that have opened the funicles can be seen with the naked eye as hook-shaped projections. Many species of the family also have conspicuous

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[1] Assisted by National Science Foundation Grant DEB77-04300 (W. G. D'Arcy, principal investigator).

[2] This work was initiated during a National Science Foundation Science Faculty Fellowship at the Missouri Botanical Garden and continued with support by a grant from Grinnell College.

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0026-6493/78/0155–0284/$13.15/0

imbricate bracts subtending the flowers. These bracts may be green, yellow, bright red, or orange.

While most genera of this family are restricted to either the New or Old World, a few are found in both. These include *Justicia* and *Ruellia*, the largest genera in the family with about 410 and 250 species respectively. Typically, most of these species are found in the tropics and subtropics with a few extending into temperate areas.

The major economic importance of the family is horticultural. Cultivation is often restricted to greenhouses, however, since, although many genera have very attractive foliage and flowers, they are difficult to grow. *Justicia guttata*, the shrimp plant, with its showy spikes of reddish brown bracts is perhaps the best known in the United States. Seeds of *Thunbergia alata*, the clock vine or black-eyed susan, are frequently sold in gardening stores in the United States, and in the tropics several other species of *Thunbergia* are grown as ornamentals. Several species of *Ruellia* are grown for their showy leaves and flowers. *Fittonia* and *Strobilanthes* are grown for sale. Many other genera are also cultivated and these include: *Acanthus*, *Aphelandra*, *Crossandra*, *Eranthemum*, *Graptophyllum*, *Hypoestes*, *Justicia*, *Pachystachys*, and *Sanchezia*.

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a. Fertile stamens 4.
  b. Plants usually scandent; seeds not borne on hooklike funicles.
    c. Fruit a drupe ..... 21. *Mendoncia*
    cc. Fruit a beaked capsule with 2–4 seeds ..... 32. *Thunbergia*
  bb. Plants not scandent, usually erect herbs or shrubs; seeds borne on hooklike funicles or if on papilliform funicles, capsule not beaked.
    d. Seeds on papilliform funicles; seeds spheroidal, not flattened; cystoliths absent in leaves.
      e. Leaves small, under 4 cm long; corolla small, under 1 cm long ..... 29. *Staurogyne*
      ee. Leaves large, over 8 cm long; corolla larger, over 1 cm long ..... 1. *Aphelandra*
    dd. Seeds on hooklike funicles; seeds flattened; cystoliths present in leaves, at least on upper surfaces (excepting *Aphelandra*).

f. Anthers 2-celled in at least one pair of stamens.
g. Upper pair of stamens with 2-celled anthers, one of the cells superposed, the shorter pair of stamens with 1-celled anthers; individual hairs of stems, leaves and bracts with a purplish banding pattern ---------- 15. *Herpetacanthus*
gg. Both pairs of stamens with 2-celled anthers, superposed or not; hairs of stem, leaves, and bracts lacking purplish banding pattern.
h. Calyx segments very dissimilar, the posterior and anterior ones much larger than the lateral ones.
i. Corolla 2-lipped, 5 mm long, white or violet; leaves under 10 cm long ---------- 30. *Teliostachya*
ii. Corolla with 5 nearly equal lobes, 15 mm long, yellow (purplish when dry); leaves over 10 cm long -- 3. *Barleria*
hh. Calyx segments similar or nearly so.
j. Shrubs or small trees; calyx segments often rounded or obtuse at tip.
k. Basal lobes of the anther rounded, not spurred; capsules 4-seeded, sericeous ---------- 33. *Tricanthera*
kk. Basal lobes of the anther spurred; capsules 8-seeded, glabrous ---------- 5. *Bravaisia*
jj. Herbs, often more or less suffrutescent (rarely shrubs;) calyx segments subulate or lanceolate, usually acute or acuminate.
l. Flowers solitary or fascicled; capsules without stalks, cylindrical; corollas 1 cm long or less.
m. Corollas white; capsules with 12–16 seeds ----- ---------- 16. *Hygrophila*
mm. Corollas blue or pale purple; capsules with 2–4 seeds ---------- 9. *Dyschoriste*
ll. Flowers mostly in spikes, racemes, cymes, or panicles (excepting axillary flowers of *Ruellia geminiflora*, *R. praeclara*, and *R. metallica*); capsules with stalks, clavate or elliptic; corollas over 1 cm long.
n. Flowers in closely imbricate bracted, 4-sided spikes; bracts conspicuous, ovate.
o. Leaves cordate; bracts indigo upon drying ---------- 14. *Hemigraphis*
oo. Leaves ovate, lanceolate or oblong lanceolate; bracts greenish upon drying -- 4. *Blechum*
nn. Flowers otherwise; bracts mostly inconspicuous and linear.
p. Inflorescences in 1-sided racemes; corollas yellow with purplish throats ------- 2. *Asystasia*
pp. Inflorescences in cymes, heads, panicles, spikes or flowers axillary; corollas variously colored, not yellowish with purple throats ---------- 27. *Ruellia*

ff. Anthers 1-celled.
q. Corolla bilabiate; stamens exserted with filaments over 10 mm long ---------- 1. *Aphelandra*
qq. Corolla lobes subequal, spreading; stamens included with filaments less than 5 mm long ---------- 23. *Neriacanthus*

aa. Fertile stamens 2.
r. Anthers 1-celled.
s. Corolla blue; upper lip of corolla over 15 mm long ---------- 12. *Habracanthus*
ss. Corolla orange or red; upper lip of corolla under 15 mm long.
t. Bracts and bractlets conspicuously shorter than calyx segments (2–3 times); corolla beaked at tip prior to expansion ---------- 18. *Kalbreyeriella*
tt. Bracts and bractlets not conspicuously shorter than calyx segments (equal to or slightly longer); corolla not beaked at tip prior to expansion.

u. Inflorescence a narrow, spike-like thyrse; some flowers borne in fascicles of 2 or 3 ..... 26. *Razisea*
uu. Inflorescence paniculate; flowers all borne singly ..... 13. *Hansteinia*
rr. Anthers 2-celled.
v. Inflorescence condensed, head-like; bracts white-ciliate, linear subulate.
w. Calyx segments 4; corolla ca. 15 mm long ..... 7. *Chaetothylax*
ww. Calyx segments 5; corolla over 20 mm long ..... 6. *Chaetochlamys*
vv. Inflorescence open, bracts otherwise.
x. Cystoliths lacking in the leaves; seeds not borne on hook-like funicles.
y. Bracts large and showy, over 30 mm long; corolla over 30 mm long ..... 20. *Megaskepasma*
yy. Bracts small and inconspicuous, under 10 mm long; corolla under 15 mm long.
z. Bracts stiff and awn-tipped; leaves mostly over 10 cm long ..... 10. *Elytraria*
zz. Bracts flaccid and awnless; leaves mostly under 8 cm long ..... 22. *Nelsonia*
xx. Cystoliths present in the leaves; seeds borne on hooklike funicles.
A. Staminodes present.
B. Anther cells basally spurred; flowers in fascicles of 6–8, loosely enclosed by bracts ..... 28. *Sanchezia*
BB. Anther cells not basally spurred; flowers not in fascicles that are enclosed by bracts.
C. Corolla limb equally or subequally 5-parted.
D. Bracts conspicuous with spiny margins, over 2 cm long; calyx segments unequal ..... 3. *Barleria*
DD. Bracts inconspicuous without spiny margins, under 1 cm long; calyx segments equal .. 25. *Pseuderanthemum*
CC. Corolla limb 2-lipped.
E. Leaf blades mottled; corolla over 7 cm long; cultivated plants ..... 11. *Graptophyllum*
EE. Leaf blades green; corolla under 6 cm long; mostly wild plants ..... 24. *Odontonema*
AA. Staminodes absent.
F. Outer bracts 4-ranked, large; flowers borne in very dense spikes.
G. Bracts under 2 cm long; calyx segments similar ..... 31. *Tetramerium*
GG. Bracts over 2 cm long; calyx segments widely dissimilar ..... 3. *Barleria*
FF. Bracts not 4-ranked, usually small; flowers borne in lax spikes, panicles, cymes, or thyrses.
H. Stems 6-angled in cross-section; calyx subtended by two partially united bracts ..... 8. *Dicliptera*
HH. Stems rounded to 4-angled; bracts distinct.
I. Calyx 5-parted.
J. Bracts large, to 44 mm long .... 20. *Megaskepasma*
JJ. Bracts small, less than 20 mm long .... 17. *Justicia*
II. Calyx 3-parted ..... 19. *Louteridium*

1. APHELANDRA

Aphelandra[4] R. Br., Prodr. Fl. Nov. 475. 1810. TYPE: *Justicia pulcherrima* (Jacq.) H.B.K.

Shrubs or suffrutescent *herbs*. *Leaves* opposite; blades usually large, oblong to elliptic, the margins toothed, lobed, crenate or entire. *Inflorescences* of terminal or axillary spikes, the spikes often conspicuous with showy bracts and flowers;

[4] For a list of synonyms see Wasshausen (1975).

bracts most often imbricate, some species bearing dorsal clusters of submarginal glands which may be conspicuous, the margins of the bracts entire, toothed or ciliate; bractlets various, rudimentary in a few species. *Flowers* with 5-merous calyx, the segments separate nearly to the base, frequently lanceolate and striate veined, the posterior segment usually broader than the others; corolla straight or curved, the limb usually bilabiate, the upper lip erect, bilobed or entire, the lower lip reflexed or spreading, 3-lobed, the middle lobe often larger than the laterals; stamens 4, usually exserted, but usually not beyond the upper lip of the corolla, the anthers narrow, 1-celled, often pilose dorsally and held together at the apices by the intertwining hairs; capsules usually clavate, 4-seeded.

Aphelandra is one of the larger genera of the family and is endemic to tropical America. Species of the genus are often quite showy, and yet they are seldom cultivated because of difficulties in cultivation. The leaves of this genus lack the cystoliths which characterize most genera of the family. The submarginal glands appearing on the bracts of many species have been observed in the field and in the greenhouse as extra-floral nectaries in *A. deppeana* and *A. pulcherrima*. This observation suggests that these glands should not be referred to as ocelli as in Leonard (1951–1958) and Wasshausen (1975).

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a. Bracts toothed.
  b. Bracts with submarginal glands.
    c. Leaves narrow, not over 2 cm wide; corolla to 5 cm long ..... 8. *A. dukei*
    cc. Leaves ovate to elliptic, to 8 cm wide; corolla to 3 cm long ..... 6. *A. deppeana*
  bb. Bracts without submarginal glands.
    d. Bracts under 15 mm long; corolla less than 2 cm long.
      e. Leaves mostly under 10 cm long; bracts over 12 mm long .. 15. *A. seibertii*
      ee. Leaves 10 cm long; bracts under 9 mm long.
        f. Leaves pilose (shaggy, soft hairs) on both surfaces; rachis of the inflorescence with numerous glandular hairs ..... 18. *A. tonduzii*
        ff. Leaves sparingly strigose (appressed, straight hairs) above, strigose only at the veins beneath; rachis eglandular ..... 1. *A. arnoldii*
    dd. Bracts over 20 mm long; corolla over 5 cm long ..... 2. *A. aurantiaca*
aa. Bracts entire.
    g. Bracts with submarginal glands.
      h. Submarginal glands consisting of dense clusters of numerous, minute glands appearing as a dull alveolar spot.
        i. Bracts over 20 mm long; calyx segments not conspicuously longer than the bracts ..... 5. *A. darienensis*
        ii. Bracts under 20 mm long; calyx segments conspicuously longer than the bracts.
          j. Corolla glabrous; bractlets over 3.5 mm wide .. 10. *A. hartwegiana*
          jj. Corolla puberulous or papillose; bractlets under 3.5 mm wide.
            k. Flowering spike expanded; bracts not imbricate .. 11. *A. laxa*
            kk. Flowering spike compressed; bracts imbricate.
              l. Petioles short, to 1 cm long; corolla puberulous ..... 12. *A. lingua-bovis*
              ll. Petioles 2–8 cm long; corolla papillose.
                m. Bracts apically acuminate to acute; calyx under 12 mm long ..... 14. *A. pulcherrima*

mm. Bracts apically obtuse; calyx over 15 mm long.
n. Leaves crenate; bracts over 10 mm wide ..... 4. *A. crenata*
nn. Leaves entire to undulate; bracts less than 10 mm wide ..... 3. *A. campanensis*

hh. Submarginal glands represented by 1 or more well-defined elliptical, shiny areas.
o. Bracts over 15 mm long; stem densely velutinous .. 16. *A. sinclairiana*
oo. Bracts 10 mm long or less; stems hirsute, but not velutinous.
p. Calyx conspicuously longer than the bracts.
q. Corolla puberulous, without papilli; flowering spike expanded; bracts not imbricate ..... 9. *A. gracilis*
qq. Corolla papillose; flowering spike compressed; bracts imbricate ..... 14. *A. pulcherrima*
pp. Calyx not conspicuously longer than the bracts.
r. Stem densely pilose; lower surface of leaf blades pilose ..... 13. *A. pilosa*
rr. Stem hirsute or strigose, but not densely pilose; lower surface of leaf blades strigose or glabrous .... 17. *A. terryae*

gg. Bracts without submarginal glands.
s. Bracts over 3 cm long; corolla over 3 cm long ..... 7. *A. dolicantha*
ss. Bracts under 1 cm long; corolla under 2 cm long.
t. Leaves apically acute, the lower surface strigose on the veins only; corolla red ..... 1. *A. arnoldii*
tt. Leaves apically acuminate, the lower surface pilose; corolla white, becoming purplish with age ..... 18. *A. tonduzii*

1. **Aphelandra arnoldii** Mildbr., Notizbl. Bot. Gart. Berlin-Dahlem 11: 63. 1930. TYPE: Colombia, *Schultze 771* (B?, not seen).

Herbs; stems short, to ca. 60 cm tall, subquadrangular, sparingly strigose. *Leaves* subrosulate, crowded, elliptic, to 18 cm long, 6.5 cm wide, apically acute, basally attenuate, sparingly strigose above, strigose only on the veins beneath, ca. 14 pairs of lateral veins, arched and ascending, the margins undulate; petioles sericeous, to 6.5 cm long. *Inflorescences* in spikes, rising from the axils of crowded terminal leaves, to ca. 24 cm long and ca. 0.5 cm wide; peduncle strigose, one bract subtending each flower, barely imbricate, erect and spreading, lanceolate, to 8 mm long and 2 mm wide, apically acute, 3-nerved with one or two lateral teeth, the longer one ca. 0.5 mm long toward the apex, the outer surface velutinous with occasional glandular hairs, the margins ciliate; bracteoles 2 subtending each flower, subulate, ca. 4 mm long and 0.8 mm wide, puberulent and with a few long glandular hairs. *Flowers* sessile; calyx segments unequal, all lanceolate and ca. 5 mm long, the anterior and lateral segments ca. 8 mm wide, the posterior segment ca. 1.4 mm wide, all segments with glandular hairs on the outside mostly toward the apex; corollas red or pink, bilabiate, ca. 1.4 cm long, 1.5 mm wide, the lateral lobes of the lower lip ca. 3.5 mm long, 3 mm wide, cuneate at the base, suborbicular, the middle lobe obcordate, 4.5 mm long, 4 mm wide, cuneate at the base, the upper lip 3 mm long, 3.5 mm wide, obcordate, the corolla glabrous outside, villous in the mouth and down the tube; stamens included, paired, the anthers held together dorsally by interweaving hairs, 1.3 mm long; ovary 1.5 mm long, the style 5.5 mm long, puberulent toward the base. *Capsules* clavate, to 10 mm long, 4 mm wide, glabrous, shiny; seeds 4, orbicular, flattened, 2 mm wide, the surface hispidulous.

This species is found in damp areas of wooded mountain slopes and cloud forests in Panama, Colombia, and northern Venezuela.

CHIRIQUÍ: Boquete, 6000 ft, *Dwyer 7028* (MO). NW of Boquete, Cerro Horqueta, 5000–5800 ft, *Dwyer et al. 468* (MO). Palo Alto just E of Boquete, 5000 ft, *Stern et al. 1057* (MO).

2. **Aphelandra aurantiaca** (Scheidw.) Lindl., Bot. Reg. 31: *pl. 12.* 1845.

Hemisandra aurantiaca Schiedw., Bull. Acad. Roy. Sci. Bruxelles 9: 22.1842. TYPE: Grown from seed of Mexican collection (not seen).

Suffrutescent *herb* to *shrub*, erect, 1 m tall; young stems tetrangular, older stems terete; younger stems glabrous to velutinous. *Leaves* elliptic, 8–30 cm long, 3–12.5 cm wide, apically acuminate, basally attenuate, occasionally obliquely decurrent, glabrous except for occasional puberulence along the veins, the costa and lateral veins prominent, reticulations plainly visible on the upper surface and obscure on the lower margins, undulate to entire; petioles to 1 cm long, glabrous. *Inflorescences* in mostly terminal, quadrifarious spikes, to 15 cm long and 2 cm wide excluding the corollas; rachis puberulous, flattened at the nodes. *Flowers* sessile; 1 bract subtending each flower, imbricate, elliptic or ovate, to 3 cm long by 1 cm wide, the apex acute, the base cuneate, puberulous-glandular on both surfaces, reticulations prominent on the inner surface, the margins ciliolate, serrate, the teeth to 1.5 mm long; 2 bracteoles subtending each flower, narrowly lanceolate, to 10 mm long and 0.5 mm wide, puberulous on both surfaces, striate ridged; calyx 5-merous, 1 cm long, the posterior segment oblong, 2.5 mm wide with a 3-toothed apex, the lateral and anterior segments linear-lanceolate, 1 mm wide, all segments puberulous with striate ridges culminating at the base in callus tissue ca. 1 mm thick; corolla red, orange red, or scarlet, the tube to 4 cm long and 3 mm wide, bilabiate, the upper lip to 2 cm long and 1 cm wide above base, oblong-ovate, apiculate at the apex, forming a partial hood over the anthers, the lower lip 3-lobed, elliptic, the middle lobe 2 cm long, 1.2 cm wide, the apex acute, the lateral lobes elliptic ovate, to 1.2 cm long and 0.75 cm wide, the apex acute, puberulous on both surfaces; style to 4.6 cm long, sparingly puberulous with ascending hairs, the ovary puberulous at the apex. *Capsules* 1.6 cm long, sparingly puberulous; seeds hispidulous.

This species is found in dense forests from Mexico to Bolivia (Leonard, 1958).

BOCAS DEL TORO: Station Milla 7.5 on Changuinola–Almirante RR, *Croat 38108* (MO). Forest above RR stop at Milla 7.5, *Croat & Porter 16260* (MO). Hillside above Almirante, *Gentry 2749* (DUKE). Changuinola, *Kennedy 3257* (MO). Chiriquicito to 5 mi S along Río Guarumo, *Lewis et al. 2078* (MO). Almirante, *McDaniel 5139* (MO). Station Milla 7.5 on Changuinola–Almirante RR, *Nee & Hanson 14090* (MO). Along trail to Risco Abajo, 3 km SW of Almirante, 100–200 m, *Nee & Hanson 14111* (MO). Water Valley, Chiriquí Lagoon, *Wedel 967, 1161, 1475, 1602* (all MO). Fish Creek Mountains, Chiriquí Lagoon, *Wedel 2302, 2326* (both MO). COCLÉ: Hills N of El Valle de Antón, trail to La Mesa, ca. 1000 m, *Allen 2711, 3694* (both MO). VERAGUAS: Santa Fé, forested slopes of Cerro Tute, 2500 ft, *Allen 4374* (MO). 5 mi W of Santa Fé on road past Escuela Agrícola de Alto Piedra on Pacific side of divide, 800–1200 m, *Croat 23038* (MO). NW of Santa Fé, 1 km from Escuela Agrícola Alto de Piedra, *Mori & Kallunki 4862* (MO).

3. **Aphelandra campanensis** Durkee.[5] TYPE: Panama, *Croat 12125* (MO, holotype; NY, isotype).

Shrub to 3.5 m tall; stem quadrangular, strigose, the lenticels corky, elliptic, ca. 1 mm long. *Leaves* elliptic, to 30 cm long and 12.5 mm wide, apically acuminate, basally attenuate, mostly glabrous to sparingly strigose above, strigose beneath, denser along veins, the margins entire or undulate; petioles to 5 cm long, strigose. *Inflorescences* in terminal spikes, borne singly or in clusters, quadrangular, to 19 cm long, 1–1.5 cm wide; rachis glabrate; bracts rhombic ovate, 10–11 mm long, 7–8 mm wide, apically obtuse to acute, apiculate, glabrate and minutely roughened with strigose hairs in some, the nerves prominent except toward the tip, with 2 submarginal glandular areas at about the midpoint consisting of a compact cluster of numerous, minute, dull, brown glands making an elliptic, alveolar spot 1.5–2.0 mm long and 0.5–0.75 mm wide, the margins subhyaline, entire; bracteoles falcate lanceolate, 9–10 mm long, 2.5–3.25 mm wide, keeled, striate nerved, densely hirsute along the keel, the marginal area glabrous, subhyaline, sparingly papillose. *Flowers* with the calyx segments conspicuously longer than the bracts, 15–17 mm long, apically obtuse, apiculate, striate nerved, glabrous outside, minutely roughened toward the apex inside, the anterior segments oblong-lanceolate, 4.5 mm wide, the lateral segments lanceolate, 3.5 mm wide, the posterior segment ovate, 7 mm wide; corolla orange red, bilabiate, densely papillate outside and inside, the tube to 4 cm long, 5 mm wide at the base, constricted to 3.5 mm wide just above the apex of the ovary, expanding to 11 mm wide at the throat, the upper lip erect, ca. 19 mm long, 9 mm wide, ovate, apically with 2 acuminate lobes ca. 6 mm long, the lower lip spreading at maturity, the middle lobe ovate, to 23 mm long, 11 mm wide, apically acuminate, the tip keeled, the lateral lobes triangular, the free portion 1.5 mm long, 2 mm wide, fused to the upper lip for most of their length, the tip rounded; stamens extending to tip of upper lip, the anthers 9 mm long, 1.5 mm broad, acute at both ends; style and ovary glabrous. *Capsules* ovate, ca. 20 mm long, 6 mm broad, the tip rounded, the surface shiny and puncticulate; seeds suborbicular, 4 mm in diameter, the surface minutely roughened.

This species is found in the provinces of Coclé and Panama in moist forest regions at ca. 1,000 m elevation. This species most closely resembles *Aphelandra chaponensis*, an endemic species of Colombia, but differs in its slightly longer and densely papillate corolla, longer and wider middle lobe of the lower corolla lip, wider bracteoles, and eciliate bracts.

BOCAS DEL TORO: 3–6 km W of Almirante, 30–200 m, *Croat 38222* (MO). CANAL ZONE: US Army Tropic Test Center, Fort Clayton, *Garner 26* (DUKE). COCLÉ: Below Cerro Pilón, *Croat 13465* (MO). Hills above El Valle de Antón, *D'Arcy & D'Arcy 6770* (MO). La Mesa, *Dwyer & Duke 8271* (MO). Above El Valle, 1000 m, *Gentry 5688* (MO). La Mesa, N of El Valle, 1000 m, *Gentry 6844* (MO). La Mesa above El Valle, 900 m, *Gentry 7407* (MO). Cerro Pilón, *Lallathin 5067* (MO). El Valle de Antón, 1000–2000 ft, *Lewis et al. 2557* (MO). Trail to Las Minas, 2.8 mi NW of church in El Valle de Antón, 3100 ft, *Luteyn 4062* (DUKE).

[5] *Aphelandra campanensis* Durkee, sp. nov. Frutex *Aphelandra chaponensis* simile sed differt ab illa corolla longiore et dense papillosa lobo medio labii inferioris longiore latioreque, bracteolis latioribus bracteis eciliatis.

Road from village of El Valle to La Mesa, 2400–2600 ft, *Spellman et al. 578* (MO). La Mesa, above El Valle de Antón, 1000 m, *Weaver & Foster 1648* (DUKE). COLÓN: Río Guanche, *D'Arcy 9677* (MO). PANAMÁ: Cerro Campana, 3000 m, *Croat 12125* (MO, NY). Cerro Campana, cloud forest, *Lewis et al. 3059* (MO). Cerro Campana, 8.6 mi SW of Capira, ca. 700 m, *Luteyn 980* (DUKE). Cerro Campana, 1 km past Su Lin Motel, *Mori & Kallunki 2450* (MO). Gorgas Memorial Labs, 25 km NE of Cerro Azul on Río Piedras, 550 m, *Mori & Kallunki 3284* (MO). Summit of Cerro Campana, *Porter et al. 4966* (MO, SCZ, US). VERAGUAS: Valley of Río Dos Bocas on road between Alto Piedra and Calovebora, 350–400 m, *Croat 27356* (MO).

4. **Aphelandra crenata** Leonard, Contr. U.S. Natl. Herb., 5: 31. 1958. TYPE: Colombia, *Haught 1464* (US).

Shrubs to 2.6 m tall; stems quadrangular toward the tip, strigose. *Leaves* oblong-elliptic, to 38 cm long and 13 cm wide, apically acuminate, basally attenuate, glabrous above, strigose beneath, the costa and the lateral veins prominent below, with 17–22 pairs of lateral veins, the margins crenate except for the basal portions; petioles 2–8 cm long, strigose. *Inflorescences* of terminal spikes borne singly and in clusters, to 24 cm long and 1.5 cm wide; peduncles ca. 2 cm long, glabrous to sparingly strigose, the lateral spikes to 14 cm long; rachis glabrous; bracts imbricate, ovate-rhombic, 13 mm long, 14 mm wide, apically obtuse and apiculate, scarlet in living plants, drying dark brown near the margins, glabrous, with 2 dull, alveolate, submarginal glandular areas midway from the base, ca. 3.5 mm long and 2 mm wide; bractlets falcate, to 11 mm long and 4 mm wide, apically acute, keeled, sericeous along the keel. *Flowers* with the calyx to 2 cm long, the segments oblong, apically rounded and slightly apiculate, glabrous, striate nerved, the posterior segment 8 mm wide, the anterior segments 5.5 mm wide, the lateral segments 4.5 mm wide; corolla rose to yellowish, to 6 cm long, 5 mm wide at the base, 8 mm wide at the throat, the upper lip erect, 18 mm long, 12 mm wide, apically bilobed, each lobe acute, ca. 8 mm long and 6 mm wide, the middle lobe of the lower lip spreading, oblong, to 18 mm long and 11 mm wide, apically obtuse, the lateral lobes ca. 6 mm long, partially adnate to the upper lip, the free portion 2 mm long, 1.5 mm wide, apically obtuse, the entire corolla papillate outside, wooly inside where the filaments join the corolla tube; stamens exserted ca. 1 cm beyond the throat. *Capsules* and the seeds not observed.

This species is found in lowland rain forests of Panama and Colombia. It is closely related to *A. hartwegiana*, but differs in its strongly crenate leaves, apically obtuse calyx segments, shorter bracts, and in some specimens, rose-colored corollas.

BOCAS DEL TORO: Little Bocas, Chiriquí Lagoon, *Wedel 2501* (MO). DARIÉN: Río Chico, Yaviza, *Allen 5094* (MO).

5. **Aphelandra darienensis** Wasshausen, Phytologia, 25: 480. 1973. TYPE: Panama, *Duke & Elias 13756* (US).

Low suffrutescent *shrub*; stems terminally subquadrangular, strigose. *Leaves* oblong-elliptic, 28–36 cm long, 13–16 cm wide, apically short-acuminate, basally acute, glabrous to sparingly strigose above, strigose beneath, more densely strigose on the costa and lateral veins, the costa and lateral veins prominent, but more so beneath, the margins entire; petioles 2.5–8 cm long, ridged, strigose. *Inflores-*

cences of terminal or axillary spikes borne singly or in clusters, 8–12 cm long, to 4 cm wide excluding the corollas, moderately compact; peduncle ca. 1 cm long, strigose; rachis glabrous; bracts imbricate, spreading with age, orange or red, rhomboid-ovate to ovate, 25–30 mm long, 10–15 mm wide, apically acute to obtuse, often crisped and retrorse, glabrous, with 2, dull, elliptic, alveolate, submarginal glandular areas just above the middle, ca. 4 mm long and 1 mm wide, the margins entire, ciliolate; bractlets lanceolate, 8 mm long, 2 mm wide, keeled, striate nerved, the keel pubescent, especially so toward the apex. *Flowers* with the calyx segments lanceolate, to 16 mm long, striate nerved, glabrous, glandular-punctate on both surfaces, the posterior segment to 6 mm wide, the anterior pair 3 mm wide, the lateral pair 2.5 mm wide; corolla orange red, to ca. 6 cm long, densely glandular-puberulous, the tube 5.5 cm long, basally 3 mm wide, 7 mm broad at the throat, the upper lip erect, oblong, 15 mm long, 2-lobed, the lobes triangular-ovate, 6 mm long, acute, the lower lip 3-lobed, the middle lobe oblong, 15 mm long, 8 mm wide, the lateral lobes similar but shorter; stamens exserted, nearly reaching the tip of the upper lip, the anthers 9 mm long, basally apiculate. *Capsules* clavate, glabrous, densely and minutely pitted, drying dark brown, ca. 3.3 cm long, 6 mm wide, 6 mm thick; seeds dark brown, unevenly oblong, 6 mm long, 4 mm wide, muricate.

This species is found in premontane to mossy forests at elevations above 600 m. Most of the corolla description and measurements were obtained from Wasshausen (1973).

DARIÉN: Ascent of Cerro Pirre from Río Pirre S of El Real, 600–750 m, *Duke 5315* (MO). Cerro Pirre, *Duke & Elias 13756* (US). Premontane rain forest between Tres Bocas and Cerro Campamiento on Cuasi-Cana Trail, *Kirkbride & Duke 1350* (MO).

6. **Aphelandra deppeana** Schlecht. & Cham., Linnaea 5: 96. 1830. TYPE: Mexico, *Schiede & Deppe* (B, destroyed, not seen).

A. pulcherrima H.B.K., Nov. Gen. Sp. Pl. 2: 236. 1817. TYPE: Mexico, *Schiede & Deppe* (B, destroyed (not seen)).
A. pectinata Willd. ex Nees in DC., Prodr. 11: 298. 1847. SYNTYPE: Mexico, *Schiede & Deppe* (W, not seen).
A. haenkeana Nees in DC., Prodr. 11: 298. 1847. SYNTYPE: Mexico, *Andrieux 131* (K, not seen).

Shrubs to 4 m high; young stems subquadrangular to terete, glabrous to velutinous, the internodes 3–10 cm long, the lenticels oval to linear, mostly under 1 mm long. *Leaves* elliptic to 22 cm long and 8 cm wide, apically acuminate, basally attenuate, glabrous to scabridulous above and strigose to velutinous beneath, especially on the costa and lateral veins, the margins entire to undulate; petioles to 5 mm long or wanting, strigose. *Inflorescences* in dense terminal spikes to 19 cm long, ca. 1 cm wide; bracts 1 per flower, elliptic, imbricate, to 15 mm long and 6 mm wide, acuminate at the apex, cuneate at the base, strigose outside, puberulous inside, with 2 clusters of submarginal, middorsal glandular areas of 1 to 10 ovular glands per area, each gland ca. 0.5 mm long, bract rather strongly 5-nerved outside, with 4–8 marginal teeth to 1.5 mm long, the margins ciliate; 2 bracteoles subtending each flower, lanceolate, to 6 mm long and 1.5 mm keeled,

velutinous along the keel; rachis pilose. *Flowers* sessile; calyx segments, lanceolate, ca. 8 mm long, the 2 anterior segments ca. 1.5 mm wide, the 2 lateral segments ca. 1 mm wide, the posterior segment ca. 3 mm wide, puberulous toward the apex; corollas pink, purplish red, scarlet or red, bilabiate, to 3 cm long, gradually expanding to 4 mm wide at the mouth, constricted to 2 mm wide just above the ovary, puberulous outside, glabrous inside, the lips ovate, the upper lip 2-lobed, ca. 1 cm long, each lobe acuminate, 3 mm long, the lower lip slightly longer, acuminate at the apex; stamens with hispid filaments, exserted. *Capsules* elliptic, to 15 mm long, 6 mm wide, 3 mm thick, the apex acute, glabrous to sparingly puberulous; seeds 2 per locule, flattened, irregular in shape, ca. 3 mm across and 1 mm thick, the surface minutely roughened, dark brown.

This species occurs in shaded areas within rain forests or secondary growth, along river banks or adjacent slopes. Generally collections are from lower elevations, although some have been collected as high as 1,600 m. It ranges from southern Mexico to northern South America and in the West Indies.

CANAL ZONE: Near water reservoir W of Cocoli, *Croat 9159* (MO). Road S-2 between Ft. Sherman and Gatun Locks, *Croat 14151* (MO). Along road to treatment plant near Miraflores Locks, *Croat 12729* (DUKE). Panamerican Highway near La Chorrera, *D'Arcy 9435* (MO). Ft. Clayton near old hospital area, *Dwyer 3891* (MO). Balboa Heights, *Greenman & Greenman 5020, 5031* (both MO). Along Panamerican Highway between Rodman Marine Base and Chorrera, *Nowicke et al. 3582* (MO). Albrook, U.S. Army Tropic Test Site, *Robyns & Dwyer 55* (MO). 1 mi SW of Cocoli in the Rodman Naval Ammunition Depot, *Wilbur et al. 12893* (DUKE). CHIRIQUÍ: 12.4 mi N of David, *Lewis et al. 718* (MO). COCLÉ: El Valle de Antón, 1000–2000 ft, *Lewis et al. 2595* (MO). Potrero, *Puga 18* (MO). Sonadora, Penonomé, *Puga 45* (MO). COLÓN: Santa Rita Ridge, *Dwyer & Correa 8424* (DUKE). Santa Rita Ridge, 2–3 mi from Transisthmian Highway, *Gentry 1857* (MO). Santa Rita Ridge E of Transisthmian Highway, 300–500 m, *Gentry 6597, 6601* (both MO). Santa Rita Ridge Road, 4 mi from Transisthmian Highway to Agua Clara weather station, ca. 500 m, *Gentry et al. 8858* (MO). Santa Rita Ridge Road, ca. 8.5 km from Boyd–Roosevelt Highway, *Mori & Kallunki 2104* (MO). Lumber road ca. 8 km NE of Santa Rita along ridge, 650 ft, *Wilbur & Weaver 10857* (DUKE). Santa Rita Ridge ca. 7 mi from Transisthmian Highway, 650 ft, *Wilbur et al. 15078* (DUKE). DARIÉN: Forest 1–3 mi N of Paya, *Duke & Kirkbride 14010* (MO). S of El Real, on slopes of Cerro Pirre ca. 3 mi E of Dos Bocas of the Río Pirre, 500–1000 m, *Foster & Kennedy 1263* (DUKE). Second large point just before Punto Alegre NE of Garachine, *Gentry 4055* (MO). Summit of Cerro Pirre, 1000–1400 m, *Gentry & Clewell 7097* (MO). Trail from Pucro to Cerro Mali, between Quebrada Matia and Quebrada Pobre, ridge between Pucro and Topalisa Rivers, 150–500 m, *Gentry & Mori 13539* (MO). Pucuro, 70 m, *Mori & Gentry 4243* (MO). Cana–Cuasi Trail, Chepigana, 4000 ft, *Terry & Terry 1522* (MO). Crest of Cana–Cuasi Trail, Chepigana, 5000 ft, *Terry & Terry 1559* (MO). HERRERA: Ocú, 100 m, *Allen 4066* (MO). Hills between Las Minas and Pesé, *Burch et al. 1349* (MO). Ocú, Río Paoancho, *Stern et al. 1738* (MO). 10 mi S of Ocú, *Tyson et al. 2815* (MO). LOS SANTOS: Headwaters of Río Pedregal, 25 mi SW of Tonosí, 2500–3000 ft, *Lewis et al. 2954* (MO). Tonosí, Guanico, *Stern et al. 1854* (MO). PANAMÁ: Taboga Island, 300 m, *Allen 102* (MO). Forest above beach E of Puerto Obaldia, *Croat 16944* (MO). Along road between Panamá and Chepo, *Dodge et al. 16644* (MO). Taboga Island, *Durkee 71–161* (MO). Slopes of Cerro Jefe, *Foster & Kennedy 1872* (DUKE). Taboga Island, near sea level, *Gentry 5737* (MO). N of Chepo, road along Río Tocumen, *Hunter & Allen 218* (MO). Sea level to 10 m, *Kennedy et al. 2022* (MO). Shrub in montane forest on the road to Cerro Campana, *Lazon 5790* (MO). 2–3 mi S of Goofy Lake, road to Cerro Jefe, 2000–2200 ft, *Lewis et al. 282* (MO). Chimán, *Lewis et al. 3331* (MO). Arraiján, *Paz 11* (MO). Chivo-Chivo, *Solanilla 10* (MO). 8 km above Goofy Lake on road to Cerro Jefe, *Weaver & Foster 1492* (DUKE). Cerro Jefe, *Wilbur et al. 11316* (DUKE). Road to El Valle de Antón on outer rim of the crater ca. 18 km from Interamerican Highway, *Wilbur et al. 15582* (DUKE). SAN BLAS: Inland from airport at Mandinga, *Duke 8909* (MO). Trail E of Cangandí-Mandinga airport road, 2–5 mi S of Mandinga airport,

Duke 14763 (MO). VERAGUAS: 2 mi S of Santa Fé, *Gentry 2939* (MO). 3.9–5 mi N of Santa Fé, 500–1000 m, *Gentry 3004* (MO). 8.8 km from Escuela Agrícola Alto de Piedra, *Mori & Kallunki 3210* (MO). 7 km W of Santa Fé on new road past agricultural school, ca. 2900 ft, *Nee 11166* (MO). 1 mi W of Santiago along old Interamerican Highway, *Tyson 5178* (MO). PROVINCE UNKNOWN: *Correa 593* (MO); *Duke 2815, 6190* (both MO).

7. **Aphelandra dolicantha** Donnell Smith, Bot. Gaz. (Crawfordsville) 27: 438. 1899. TYPE: Costa Rica, *Donnell Smith 6689* (US).

Shrubs to 2 m tall; stems quadrangular, glabrous to puberulous, the hairs brownish. *Leaves* ovate to elliptic, to 17 cm long and 8.5 cm wide, apically acuminate, basally attenuate, glabrous above, glabrous to finely strigose beneath, when present the hairs more dense on costa and lateral veins, drying to a lighter green than the upper surface, the costa and lateral veins prominent, the margins entire; petioles 1–4.5 cm long, glabrous to minutely strigose. *Inflorescences* of terminal sessile spikes borne singly or occasionally in small clusters, to 8 cm long and 1 cm broad; rachis sericeous with hairs ascending; bracts closely imbricate, green when fresh, drying reddish brown, ovate-lanceolate to oblanceolate, to 3.5 cm long and 0.7–1 cm wide, apically acuminate to acute, glabrous, the margins ciliolate; bracteoles linear, to 8 mm long and 0.5 mm wide with appressed pilose hairs, 0.5 mm long. *Flowers* with the calyx minute, the segments linear-subulate, ca. 1.5 mm long, 0.25 mm long, ciliolate; corolla white, the tube slender, glandular-puberulous, to 5 cm long, nearly cylindrical, basally 2 mm broad, 3.5 mm broad at the throat, the lobes glabrous, the upper lip erect, oblong, to 12 mm long and 6 mm wide, 2-lobed, the lobes 5 mm long, 3 mm wide at the base, apically rounded, the middle lobe of the lower lip to 22 mm long, 9 mm wide, apically rounded, the lateral lobes oblong, to 17 mm long and 6 mm wide, apically rounded; stamens included, filaments ca. 6 mm long, affixed just below the throat, the anthers 2.5 mm long, basally apiculate, adhering by terminal hairs; style included. *Capsules* (from Leonard, 1958) narrowly clavate, ca. 15 mm long, 3 mm broad, glabrous, minutely punctate; seeds flattened, obliquely ovoid, 5.5 mm long, 3.5 mm broad, ca. 1 mm thick, smooth, brown.

This species is found in rain forests at lower elevations between 45 and 1,000 m, and its range extends from Colombia to Guatemala.

BOCAS DEL TORO: Between Buena Vista coffee finca and Cerro Pilón on Chiriquí trail, *Kirkbride & Duke 695* (MO). VERAGUAS: Valley of Río Dos Bocas on road between Alto Piedro and Calovébora, *Croat 27443* (MO). Valley of Río dos Bocas, 11 km from Escuela Agrícola Alto de Piedra on road to Calovébora, 450 m, *Croat 27513* (MO). Cerro Tute, ca. 10 km NW of Santa Fé, 750–1000 m, *Mori et al. 7535* (MO).

8. **Aphelandra dukei** Wasshausen, Phytologia 25: 475. 1973. TYPE: Panama, *Duke 14397* (MO).

Suffrutescent *shrub* ca. 1 m high; stems quadrangular near apex, terete in older portions, glabrous to tomentulose. *Leaves* narrowly elliptic, to 15.5 cm long and 2 cm wide, apically acuminate, basally attenuate, sparingly strigose along the costa above, strigose mostly on the costa and the lateral veins beneath, drying to dark green above, pale beneath, the margins entire; petioles (unwinged por-

tion) 0.5–1 cm long, pubescence that of the stem. *Inflorescences* in terminal spikes to 14 cm long, 2 cm wide at anthesis (excluding flowers), the bracts imbricate, the peduncles short, to ca. 0.5 cm long, pubescence as the stem, the rachis sericeous; bracts green, rhomboid-elliptic to 15 mm long, 5.5 mm wide, apically acuminate, sericeous, with two shiny, oval, submarginal clusters of 2–6 oval glands, each ca. 0.5 mm long, the margins above the middle with ca. 3 pairs of spinetipped teeth to ca. 2 mm long; bractlets lanceolate, 8–10 mm long, 1–1.25 mm wide, keeled, pilosulus mostly along the keel. *Flowers* with the calyx segments lanceolate, 9–10 mm long, striate-nerved, mostly glabrous, the margins ciliolate toward the apex, the dorsal segment 2 mm wide, the lateral pair 1.25 mm wide, the anterior pair 1.0 mm wide; corolla bright red, ca. 4 cm long, the tube sparingly puberulous and minutely papillose, 2.5 cm long, basally 2 mm wide, 4.5 mm wide at the throat, the lobes with sericeous hairs apically, the upper lip erect, oblong-ovate, ca. 15 mm long, 4.5 mm wide, 2-lobed, the lobes apically acuminate, 5 mm long, basally 2 mm wide, curved outward, the lower lip spreading, appearing 1-lobed, the lobe ca. 15 mm long, 4 mm wide, apically acuminate, the tip recurved; stamens exserted. *Capsules* green, elliptic, ca. 12 mm long, 6 mm wide, 4 mm thick, shiny, sparingly puberulous, minutely punctate; mature seeds not seen.

This species is found along sandy and rocky riverbanks of lower elevations in central Panama.

DARIÉN: Púcuro, 70 m, *Mori & Gentry 4245* (MO). PANAMÁ: Río Bayano, 1–4 mi above Piria, ca. 100 m, *Duke 14397* (MO). Tributary of Río Chagres, 5 mi SW of Cerro Brewster, ca. 1000 ft, *Lewis et al. 3426* (MO).

9. **Aphelandra gracilis** Leonard, Proc. Biol. Soc. Wash. 56: 54. 1943. TYPE: Panama, *Allen 2908* (US).

Shrub to 3 m high; stems subquadrangular near the apex, terete below, sparingly to moderately strigose with conspicuous, corky, cream colored lenticels to 0.7 mm in diameter. *Leaves* elliptic to obovate, to 18 cm long and 7.5 cm wide, apically acuminate, basally attenuate, glabrous above and beneath except for a few strigose hairs along the costa, the margins entire; petioles 0.5–1 cm long, strigose to glabrous. *Inflorescences* of terminal, subquadrangular spikes borne singly or in panicles, to 15 cm long and 1.5 cm wide at anthesis excluding the corolla; peduncles 5–7.5 mm long, strigose, the rachis puberulous, the internodes 6–8 mm long; bracts drying greenish to reddish brown, barely imbricate, subulate when fresh, oblong when flattened, 5–8 mm long, 3.5–4 mm wide, with two dorsal clusters of 3 to many, shiny, elliptic, submarginal glands ca. 0.5 mm long, 0.2 mm wide; bracteoles lanceolate, 5 mm long, 2 mm wide, puberulous. *Flowers* spreading at maturity clearly exposing the rachis; calyx puberulous, extending well above the bracts, segments lanceolate, ca. 8 mm long, apically subacute, the posterior segment 3 mm wide, other segments 2.3 mm wide, striate nerved; corolla scarlet, puberulous, the tube funnelform glabrous inside, 5.5–6 cm long, 5 mm wide at the base, 9 mm wide at the mouth, the upper lip erect to 20 mm long and 10 mm wide, 2-lobed, the lobes apically acuminate, to 8 mm long and

keeled at the apex, the middle lobe of the lower lip spreading, lanceolate, to 24 mm long and 9 mm wide, apically acuminate and keeled, the lateral lobes triangular, attached on one side to the upper lip, acute, the free portion to 1.1 mm long and 1.3 mm wide; stamens exserted, about equalling the upper lip and generally enclosed by it. *Capsule* clavate, coarsely puberulent, to 2 cm long, 6.5 cm broad above and 3 mm broad at the base, the surface muricate and shiny at maturity, apically obtuse; seeds 4, flattened, orbicular, ca. 3.5 mm in diameter and 2 mm wide.

This species is found in valleys and along streams at middle elevations in central Panama.

COCLÉ: N of El Valle de Antón, 1000 m, *Allen 1671, 2908* (both MO). El Valle, *Dwyer 1838* (MO). Road back of Club Campestre, El Valle, *Dwyer 11845* (MO). El Valle, *Gentry & Dwyer 3587* (MO). COLÓN: Santa Rita Ridge, 5.5–6 mi E of Transisthmian Highway, *Lewis et al. 5392* (MO). Santa Rita Ridge, on property of Peter & Leslie Tassel, ca. 1.9 km from Boyd-Roosevelt Highway, *Mori & Kallunki 1801* (MO). Santa Rita Ridge, *Mori & Kallunki 3025* (MO). PANAMÁ: Lower slopes above FSU cabin, Cerro Campana, 850 m, *Croat 22793* (MO). Cerro Jefe, *Duke 9394* (MO). Cerro Jefe, *Dwyer & Gentry 9458* (MO). 5–10 km NE of Altos de Pacora, *Gentry et al. 4199* (MO). Ca. 10 km N of Panamerican Highway on El Llano-Carti Road, 500 m, *Gentry et al. 8873* (MO). Near top of Cerro Jefe to 1 mi beyond, *Gentry & Tyson 3490* (MO). 10 km above Panamerican Highway on road from El Llano to Carti-Tupile, 150–350 m, *Kennedy & Dressler 2954* (MO). Cloud forest, Cerro Campana, *Maas & Dressler 726* (MO). El Llano-Carti Road, 10 km from Interamerican Highway, *Mori & Kallunki 2260* (MO). Gorges Memorial Labs, 5–10 km NE of Altos de Pacora, ca. 600 m, *Mori & Kallunki 3343* (MO). Forested slopes of Cerro Jefe near large coffee finca, *Wilbur et al. 11326* (DUKE). VERAGUAS: 5 mi W of Santa Fé past Escuela Agrícola de Alto Piedra, on Pacific side of divide, 800–1200 m, *Croat 23038* (MO). Above Santa Fé on slopes of Cerro Tute, 1200–1400 m, *Gentry 6247* (MO).

10. **Aphelandra hartwegiana** Nees in Benth., Pl. Hartw. 236. 1846. TYPE: Colombia, *Hartweg 1270* (not seen).

Shrubs to 4 m high; stems subquadrangular in younger portions, soon becoming terete, strigose to glabrate, the lenticels elliptical, ca. 1 mm long. *Leaves* oblong elliptical to oblong ovate, 25–35 cm long, 7–11 cm wide, apically acuminate, basally attenuate, glabrous to sparingly strigose above, sparingly strigose to strigose beneath, the costa and the lateral veins prominent beneath, from 11–22 pairs of lateral veins, the margins entire to slightly crenate; unwinged portion of petiole 0.5–6 cm long. *Inflorescences* terminal, solitary, or several, the spikes, to 25 cm long and 2.5 cm wide, the peduncle of terminal spike to 1.5 cm long, those of lateral spikes longer, the rachis glabrous; bracts imbricate, red to orange when fresh, drying to brown with dark brown borders, rhombic-ovate, to 16 mm long, 13 mm wide, mostly apically obtuse but some apiculate with 2 dull, alveolate, submarginal glandular areas on the upper half of the bract, 4 mm long, 1.5 mm wide, 3-nerved, glabrous, the margins entire and hyaline for 0.25–0.5 mm; bractlets falcate, to 1 cm long and 3.5 mm wide, subcarinate, apically acute, keel puberulous to hirsute, striate-nerved. *Flowers* with the calyx segments oblong, to 22 mm long, the posterior segment 9 mm wide, the anterior segments 5.5 mm wide, the lateral segments 4.5 mm wide, all apically acute and apiculate, glabrous, striate nerved; corolla yellow or orange, glabrous, the upper lip erect, lanceolate, 2 cm long, ca. 6 mm wide, apically bi-

lobed, these triangular, ca. 5 mm long, 3 mm wide, acuminate and apiculate, the middle lobe of the lower lip spreading, lance-ovate, ca. 2 cm long and 12 mm wide, apically acuminate, the lateral segments ca. 7 mm long, partly adnate to the upper lip, free portions triangular, ca. 1.5 mm long and 1 mm wide, obtuse. *Capsules* obovoid, 2.0–2.3 cm long, 7 mm wide and 5 mm thick, glabrous, nitid and punctate.

This species is found at lower elevations on forested hillsides and along streams of Colombia and Panama. Since available specimens lacked complete corollas this description was largely obtained from Leonard (1958).

BOCAS DEL TORO: Hillside above Almirante, *Gentry 2748* (MO). DARIÉN: S of El Real, headwaters of Río Pirre at a fork known as Dos Bocas, ca. 100 m, *Foster & Kennedy 1247* (DUKE). Along stream near Bartolome, *Kennedy 2832a* (MO).

11. **Aphelandra laxa** Durkee.[6] TYPE: Panama, *Mori et al. 6854* (MO, holotype).—FIG. 1.

Shrub to 1.5 m tall; younger stem quadrangular, glabrous. *Leaves* ovate-elliptical, to 35 cm long, 18.5 cm wide, apically acuminate, basally attenuate, glabrous above and beneath, drying dark green above, lighter green beneath, the margins entire to undulate; petioles to 3 cm long, glabrous. *Inflorescences* of lax terminal, sessile spikes to 18 cm long, 5–10 mm wide excluding corollas, the rachis subquadrangular, 2 mm broad, glabrous, considerably exposed by widely spaced bracts at intervals of 1.5–2.0 cm, the bracts rhombic-ovate, to 8 mm long, 6 mm wide, apically acute, with 2, dull, alveolate, submarginal glandular areas on the lower half of the bract, 2 mm long, 0.75 mm wide, glabrous, minutely ciliolate; bracteoles ovate, keeled, to 7 mm long, 2.5 mm wide, apically acute, glabrous. *Flowers* with the calyx segments conspicuously longer than the bracts, linear subulate, the segments to 11 mm long, apically acute, apiculate, striate nerved, the anterior segments ca. 3 mm wide, the lateral segments 2.5 mm wide, the posterior segment 3.5 mm wide; corolla red, bilabiate, to ca. 7 cm long, minutely puberulous inside and out, the tube to 4.2 cm long, 4 mm wide at the base, constricted to 2 mm just above the apex of the ovary, expanding to 9 mm wide at the throat, the upper lip erect, ca. 25 mm long, 8 mm wide, ovate, apically with 2 acuminate lobes ca. 11 mm long, the lower lip spreading at maturity, the middle lobe ovate, 30 mm long, 11 mm wide, apically acuminate, the lateral lobes triangular, the free portion 0.5 mm long, 0.5 mm wide, connate to the upper lip for most of their length, the tips rounded; stamens exserted to the tip of the upper lip, the anthers 7–8 mm long, 2 mm broad, acute at both ends; filaments glabrous; style and ovary glabrous. *Capsule* clavate, 16 mm long, 9 mm broad, glabrous, the surface shiny and puncticulate; seeds ovate, 5 mm long, 4.5 mm wide, minutely scabrous.

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[6] *Aphelandra laxa* Durkee, sp. nov. Frutex ad 1.5 m alta; foliis ovato-ellipticis ad 35 cm longis, 18.5 cm latis; inflorescentibus ex spicis laxis, terminalibus, sessilibus, ad 18 cm longis constantibus, rachidibus subquadrangularibus, 2 cm latis, glabris, aliquantum nudis inter bracteas semotas, spatiis 1.5–2.0 cm, bracteis duo, rhombeo-ovatis ad 8 cm longis, 6 mm latis, acutis, hebetatis, alveolatis, areas submarginales glandulares infra medium ferentibus; partibus calycis bracteas insignitur superantibus, linearo-subulatis ad 11 mm longis, corolla rubra ad 7 cm longa.

FIGURE 1. *Aphelandra laxa* Durkee. Habit (×⅝). [After *Mori 6854* (MO).]

This species is known only from type collection, found along a trail through rain forest. It resembles *A. gracilis* in its lax spikes, but differs from it in the longer internodal lengths of its spike, its alveolate glandular areas on the bracts, and its appressed bracts and flowers.

SAN BLAS: On trail to Darién from Puerto Obaldía 1–20 km WSW of Puerto Obaldía on Caribbean slope of Cordillera, *Mori et al. 6854* (MO).

12. **Aphelandra lingua-bovis** Leonard, Contr. U.S. Natl. Herb., 5: 31. 1958. TYPE: Colombia, *Archer 2012* (US).

Shrubs to 2 m tall; stems terete or subquadrangular toward the tip, moderately and minutely strigose, the hairs upwardly appressed. *Leaves* ovate elliptic to elliptic, to 28 cm long and 15 cm wide, apically acuminate and often curved to one side, basally attenuate, glabrous above, or sparingly strigose in the younger leaves, occasionally strigose or more spreading, the hairs densest along the costa and the lateral veins, the costa and the lateral veins prominent, the lower surface drying to a lighter green, the margins entire or undulate; petioles to ca. 1 cm long, strigose. *Inflorescences* of terminal spikes borne singly or in clusters, the spikes to 19 cm long and 1.5 cm wide, the rachis unevenly sericeous, the peduncle to 8 mm long, sericeous; bracts orange to bright red when fresh, drying to reddish brown, rhombic ovate, to 16 mm long and 8 mm wide, apically acute, glabrous to puberulous with upwardly appressed, strigose hairs along the costa, the costa and the lateral veins prominent with two dull elliptic, alveolate, submarginal glandular areas dorsally about midway from the base, to 3 mm and 1 mm wide, the margins ciliolate; bractlets linear lanceolate, to 17 mm long and 2 mm wide, apically acuminate, keeled, the keel densely hirsute with ascending hairs ca. 1 mm long. *Flowers* with the calyx ca. 17 mm long, the segments lanceolate, increasingly puberulous toward the apex, striate nerved, the posterior segment 8 mm wide, the lateral segments 1.7 mm wide, the anterior segments 2.2 mm wide; corolla bright red or reddish yellow, 5.5–6 cm long, puberulous, the tube subcylindric, slightly curved, 3.5 mm broad at the base and 6 mm broad at the throat, the upper lip erect, elliptic, 16 mm long, 7 mm wide, 2-lobed, the lobes apically acute, 4 mm long, 3 mm wide basally, the middle lobe of the lower lip lanceolate, 18 mm long, 6 mm wide, acute, the lateral lobes 4 mm long, partly adnate to the upper lip, the free portions triangular, ca. 1.5 mm long, 1 mm wide, apically acute; stamens slightly exserted, the anthers apiculate at both ends, webby-pilose at the tip; ovary densely strigose, the hairs ascending. *Capsules* clavate, 18–20 mm long, 4 mm wide, 3.5 mm thick, glabrous except for ascending strigose hairs toward the rounded apex; seeds 4, dark brown, deltoid, ca. 5 mm long, 4 mm wide, the margins sparingly tuberculate.

This species is found in rain forests at mid to lower elevations of Darién Province and adjacent Colombia.

COCLÉ: Along road ca. 8 mi N of El Valle de Antón, *Luteyn & Kennedy 1683* (DUKE). 3 km NE of El Valle, *Mori & Kallunki 2953* (MO). COLÓN: Río Guanche, 1–4 km upstream from Portobelo Road, 0–100 m, *Gentry 8783* (MO). Near bridge over Río Buenaventura, near Portobelo, *Foster & Kennedy 1794* (DUKE). Río Guanche, 1–4 km upstream from Portobelo Road, 0–100 m, *Mori & Kallunki 3009* (MO). DARIÉN: Ascent of Cerro Pirre from Río Pirre S of El Real, 750–1030 m, *Duke 5329* (MO). Cocalito, Pacific side near Prov. Darién's Colombia border, *Dwyer 4339A* (MO). Summit of Cerro Pirre, 1000–1400 m, *Gentry & Clewell 7110* (MO).

13. **Aphelandra pilosa** Leonard, Contr. U.S. Natl. Herb., 5: 31. 1958. TYPE: Colombia, *Cuatracesas 7223* (US, not seen).

Shrubs to 3 m tall; stems subquadrangular toward the apex, densely pilose, the hairs light brown to 2 mm long, spreading. *Leaves* elliptic, to 21 cm long and 8.5 cm wide, apically acuminate, basally attenuate, sparingly pilose above, the costa and the lateral veins densely pilose, the hairs light brown, 1–1.5 mm long, pilose beneath, venation prominent, the margins entire or undulate; petioles ca. 1.5 cm long, densely pilose. *Inflorescences* in terminal spikes borne singly or in panicles, to 9 cm long and 1 cm wide, the peduncle densely pilose as in the stems, ca. 1 cm long, the rachis white tomentose; bracts closely imbricate, dark brown upon drying, apically acute, ovate lanceolate, to 9 mm long and 6 mm wide, puberulous outside, and with strigose hairs toward the tip and along the mid-vein to the base on some bracts, with two dorsal clusters of 10–20 shiny, oval, submarginal glands each ca. 0.5 mm long, the margins of bracts ciliolate, the bracteoles ovate lanceolate, to 6 mm long and 2.5 mm wide, keeled, striate nerved, puberulous with pilose hairs along the keel toward the apex, the margins ciliolate. *Flowers* with the calyx segments to 7.5 mm long, puberulous, striate-nerved, the posterior segment ovate lanceolate, to 3.5 mm wide, the lateral segments linear lanceolate to 1.5 mm wide, the anterior segments lanceolate to 2.5 mm wide, all apically apiculate; corolla red or light bluish red, to 6.5 cm long, puberulous outside, the tube funnelform, glabrous inside, slightly curved, to 4.5 cm long, 7 mm wide at the mouth, 4.5 mm wide at the base, the upper lip erect to 20 mm long and 8 mm wide, 2-lobed, the lobes apically acuminate and keeled to 8 mm long and 4 mm wide, the middle lobe of the lower lip spreading, lanceolate, to 21 mm long and 8.5 mm wide, apically acute, the lateral lobes triangular, attached on one side to the upper lip, apically rounded, the free portion 3 mm long, 2 mm wide; stamens exserted, about equaling the upper lip and enclosed by it, the filaments puberulous toward the base, the anthers dorsally pilose and basally slightly apiculate; the pistil glabrous. *Capsules* clavate, dark brown, shiny, glabrous, to 23 mm long, 10 mm wide, 4 mm thick; seeds 2–4, oval, flattened, 7 mm long, 5 mm broad, the surface reticulate, dark brown.

This species is found in primary forest at low to mid elevations of Panama and Colombia. It is most similar to *A. pulcherrima* and differs from it mainly in its denser, longer pilose hairs on the stems, petioles and leaves.

PANAMÁ: Primary forest along newly cut road from El Llano to Cartí-Tupile, 12 mi above Panamerican Highway, 200–500 m, *Croat 2289* (MO), *Liesner 1222* (MO).

14. **Aphelandra pulcherrima** (Jacq.) H.B.K., Nov. Gen. Sp. Pl. 2: 236. 1817.

Justicia pulcherrima Jacq., Enum. Pl. Carib. 11. 1760; Stirp. Amer. 6, *pl. 2, fig. 4.* 1763. TYPE: Colombia *Jacquin* (W, not seen).

Shrubs or suffrutescent *herbs* to 5 m tall; young stems quadrangular, terete when older, glabrous to sparingly strigose, the lenticels scattered, oval, ca. 0.5 mm long, corky. *Leaves* elliptic to elliptic obovate, to 30 cm long and 11 cm wide, apically acuminate, basally attenuate, glabrous above, sparingly strigose

to glabrous beneath, the margins shallowly crenate to slightly undulate; petioles ca. 3 cm long, pubescence as on the costa. *Inflorescences* terminal, quadrangular, the spikes to 20 cm long and 1 cm wide; bracts rhombic ovate, imbricate, 7–9.5 mm long, 5–6 mm wide, apically acute to acuminate, apiculate, keeled and striate nerved, minutely puberulous on the upper bracts, the lower bracts increasingly strigose mostly over the keel, ciliolate with submarginal glandular areas just below the midpoint consisting of numerous, minute (0.2 mm) often shiny brown to dark brown glands making an elliptic, alveolar spot 1.5–2.5 mm long, 0.5–1 mm wide; bracteoles falcate, keeled, to 8 mm long, 2.5 mm wide, striate nerved, finely puberulous without except for the wooly keel, glabrous within; rachis glabrous to sparingly puberulous. *Flowers* with the calyx segments conspicuously longer than the bracts, 9–11 mm long, glabrous, lanceolate, apically acute, the anterior segments 2.5 mm wide, the lateral segments 2 mm wide, the posterior segment 4.5 mm wide, all striate nerved; corolla bright red, bilabiate, papillate outside and in, the tube to ca. 5 cm long, 4 mm wide at base, constricted to ca. 2 mm just above the apex of the ovary, gradually extending to 9 mm wide at the throat, the upper lip erect, ca. 19 mm long, basally 9 mm wide, consisting of 2 acuminate lobes ca. 8.5 mm long, the lower lip spreading at maturity, with 3 lobes, the middle lobe lanceolate, ca. 24 mm long and 7 mm wide, the lateral lobes ca. 5 mm long, acute, connate to the upper lip for most of their length; stamens extending to about the length of the upper lip. *Capsules* oblong, obtuse, glabrous.

This species is found in tropical rain forests of lower elevations ranging from Mexico to northern South America. The capsule description was obtained from Leonard's description since none were present on Panamanian specimens.

CANAL ZONE: Río Indio de Gatún, *Maxon 4807* (US). COLÓN: Path through bananas from sea to top of ridge behind Garotte, *D'Arcy 9311* (MO). Río Guanche, *D'Arcy 9696* (MO). DARIÉN: Río Aruza, *Bristan 1248* (MO). Between Río Perecenico and Rancho Frio, 500–2500 ft, *Duke & Elias E 13889* (MO). Near Cerro Pirre base camp on Río Parasenico, 200–500 m, *Gentry & Clewell 7061* (MO). Camp Summit, San Blas-Darién border along Sea Level Canal Rt. 17, 1000–1200 ft, *Oliver et al. 3676* (MO, US). PANAMÁ: 5 mi up Río Nuevo. *Foster 1993* (DUKE, US). Along Chanave River, above Chepo, 40–200 m, *Pittier 4723* (US). SAN BLAS: Beach E of Puerto Obaldía, *Croat 16890A* (MO, US). Mainland in front of Ustupo, *D'Arcy 9476* (MO). Headwaters of Río Cuadí, Camp Diablo, *Duke et al. 3611* (MO, US). Mainland opposite Ailigandí, *Lewis et al. 172* (DUKE, F, MO, US). Forests around Puerto Obaldía, San Blas coast, 0–50 m, *Pittier 4280* (NY).

15. **Aphelandra seibertii** Leonard, Ann. Missouri Bot. Gard. 24: 205. 1937. TYPE: Panama, *Seibert 460* (MO).

Herbs, erect to 19 cm high; stem quadrangular, pilose hairs to 1 mm long, the lower stem rooting at the nodes. *Leaves* elliptic to 9.5 cm long, 4.2 cm wide, apically acute, basally acute, the pilose hairs to 1 mm long above and beneath, dense along costa and lateral veins beneath, the margins entire to slightly undulate, the petioles to 1.6 cm long, densely pilose. *Inflorescences* in 1–3 terminal spikes, to 13 cm long and 1 cm wide, the rachis densely pilose; bracts closely imbricate, spreading at maturity, rhombic, to 14 mm long, 6 mm wide, the tips often purplish, the margins above the midpoint dentate with 2–3 erect teeth, ca. 1 mm long, the bractlets lanceolate 8.5 mm long, 2 mm wide, keeled, translucent, pilose along

the keel. *Flowers* falling away at time of maturity when the bracts are expanded; calyx segments translucent, with sparse small glandular hairs plus pilose hairs, lanceolate, anterior segments 5 mm long and 0.7 mm wide, the lateral segments 5 mm long and 0.5 mm wide, the posterior segment 5.3 mm long and 1.4 mm wide; corolla yellow at base, the lobes lavender tipped, bilabiate, the tube funnelform, 11 mm long, 2 mm wide at the base, 4 mm wide at the mouth, the upper lip 6.5 mm long and 5.5 mm wide, divided to 2 mm into 2 rounded lobes, the lower lip 8 mm long, with 3 lobes, the lateral lobes rounded, 6 mm long and 2 mm wide, the middle lobe retuse, 8 mm long and 5 mm wide, puberulous glandular outside, glabrous inside; stamens slightly exserted, the filaments pilose. *Capsules* oblanceolate, ca. 8 mm long, 3 mm wide and 1.5 mm thick, reddish brown; seeds 4 near-triangular, puberulent, 3 mm long and 0.7 mm thick.

Aphelandra seibertii is found in moist habitats of Costa Rica and Panama.

COCLÉ: El Valle, 600–1000 m, *Allen 1215* (MO). N rim of El Valle de Antón, 600–1000 m, *Allen 1642*; *Seibert 460; Woodson & Schery 187* (all MO).

16. **Aphelandra sinclairiana** Nees in Benth., Bot. Voy. Sulphur, 146, *pl. 47*. 1844. TYPE: Panama, Isthmus of Panama, *Sinclair* (K, not seen).

Shrubs or small *trees* to 6 m high; younger stems terete to subquadrangular at terminus, velutinous. *Leaves* narrowly elliptic to near oblanceolate, to 37.5 cm long and 10 cm wide, apically acuminate, basally attenuate, sparingly pilose above except at the costa, pilose beneath, the margins entire to shallowly crenate; petioles 1–2 cm long, pilose. *Inflorescences* borne in terminal and subterminal spikes in clusters of up to 10 spikes, spikes to 15 cm long and 2 cm wide, the rachis hispid to wooly; bracts orange red, densely imbricate, obovate rhombic, to 20 mm long, 15 mm wide, the apex of the lowermost bracts acuminate and the upper bracts obtuse, 5 or 6 prominent dorsal nerves branching toward the apex of the bract, velutinous dorsally and puberulous ventrally, with two clusters of elliptic glands toward the margins at about the middle of the dorsal surface, the glands ca. 0.5 mm long and 0.4 mm wide, 4–10 glands per cluster, the margins of the bracts entire; bracteoles lanceolate, to 7.5 mm long and 3 mm wide, striate, partially keeled toward the apex, tomentose outside, puberulous inside. *Flowers* falling away at maturity when the bracts are expanded; calyx 5-merous, all segments separate to base, lanceolate, the posterior segment to 9 mm long and 3 mm wide, the remaining segments to 9 mm long and 2 mm wide, puberulous outside and glabrous inside, striate; corolla purplish red, bilabiate, puberulous inside and outside, the tube funnelform, to 4.5 cm long, 3.5 mm wide at base, 6.5 mm wide at mouth, the upper lip erect, to 17 mm long, 9 mm wide, 2-lobed, the lobes acuminate and keeled at the apex, to 7.5 mm long, the lower lip spreading, the middle lobe lanceolate, keeled, to 25 mm long, 8 mm wide, the lateral lobes triangular, attached on one side to the upper lips, acute, the free portion to 1.3 mm long and 1.5 mm wide; stamens exserted to just below the tips of the upper lip and enclosed by it. *Capsules* clavate, to 1.8 cm long and 6 mm broad distally, 3 mm broad at the base, puberulent, obtuse at the apex; seeds 4, puberulent, flattened, ca. 3.5 mm in diameter.

This species is found in moist, open areas of rain forest and in low, wet areas of low growth in both Costa Rica and Panama.

BOCAS DEL TORO: Hillside above Almirante, *Gentry 2684* (MO). Quebrada Huron, 300–400 ft, *Kirkbride & Duke 422* (MO). Changuinola to 5 mi S at junction of Ríos Changuinola and Terebé, 100–200 ft, *Lewis et al. 803* (MO). Chiriquí Lagoon, *Wedel 762, 1012, 1083* (all MO). Garay Creek, Chiriquí Lagoon, *Wedel 2636* (MO). Water Valley, *Wedel 973* (MO). CANAL ZONE: Atlantic side along Transisthmian Highway, *Blum & Dwyer 2137* (MO). W end of Gatún Lake Dam, *Blum & Tyson 1975* (MO). Road between Gatún and Ft. Sherman, *Burch et al. 1016* (MO). Barro Colorado Island, *Croat 4650, 5157, 7297, 7760, 7836, 8574, 8624, 9441* (all MO). Roadside Madden Forest Road 1, *Croat 8952* (MO). Road C-16, NW of Pedro Miguel, *Croat 12262* (MO). Road S-10, N of Escobal, *Croat 12443* (MO). Pipeline Road 10 mi NW of gate, *Croat 12776* (MO). Forest at N edge of Summit Garden, *Croat 13129* (MO). W arm of Quebrada Salamanca, 70 m, *Dodge et al. 16996* (MO). Road K 5-17, *Duke 8968* (MO). Las Cruces Trail, *Dwyer 1958* (MO). France Field, *Dwyer 8542* (MO). Ft. San Lorenzo, *Ebinger 470* (MO). Chagres, *Fendler 209* (MO). Madden Forest Preserve, *Lewis et al. 5334* (MO). Military Reserve, Ft. Sherman, Road S-1 between Gatún and Piña, 0–170 m, *Liesner 1357* (MO). Pipeline Road, N of Gamboa, *Luteyn & Foster 1539* (DUKE). Navy Reservation N of Gamboa, *Maas & Dressler 711* (MO). Road from Ft. Sherman to Ft. San Lorenzo, *Porter et al. 4991* (MO). Barro Colorado Island, *Shattuck 372, 760* (both MO). Road K-15 near Huile on the hills around Gatún Lake, *Smith et al. 3278* (MO). 6 mi N of Gamboa, *Tyson 3501* (MO). Barro Colorado Island, *Wetmore & Abbe 2* (MO). Pipeline Road NW of Gamboa ca. 6 mi, *Wilbur & Teeri 13365* (DUKE). Pipeline Road N of Gamboa, *Wilbur & Weaver 11255* (DUKE). Barro Colorado Island, *Woodworth & Vestal 364* (MO). CHIRIQUÍ: San Bartolo Limite near Costa Rican border, 12 mi W of Puerto Armuelles, 400–500 m, *Croat 22194* (DUKE). Ca. 2 mi S of Puerto Armuelles, *Wilbur et al. 13583* (DUKE). COCLÉ: Lower Río Antón, El Valle, *Allen 125* (MO). Río Indio Trail, El Valle de Antón, 500–700 m, *Hunter & Allen 358* (MO). El Valle de Antón, 1000–2000 ft, *Lewis et al. 2614* (MO). COLÓN: Juan Mina Plantation, Río Chagres, region above Gamboa, 25 m, *Allen 4138* (MO). Portobelo, *Chan 53* (MO). Ca. 0.5 km from the Río Buenaventura, near Portobelo, *Kennedy & Gra 2239* (MO). PANAMÁ: Nuevo Emperador, *Carrasco 28* (MO). Cerro Jefe, *Duke 9394* (MO). Capira, trail between Lídice and Aguacate, 300 m, *Foster 2140* (DUKE). Tributary of Río Chagres, 5 mi SW of Cerro Brewster, ca. 1000 ft, *Lewis et al. 3386* (DUKE, MO). SE side of Madden Lake near the Puente Natural, 90 m, *Nee & Hansen 14047* (DUKE, MO). PROVINCE UNKNOWN: *Duke 6148* (MO).

17. **Aphelandra terryae** Standley, Pub. Field Mus. Nat. Hist., Bot. Ser. 22: 381. 1940. TYPE: Panama, Darién, Chepigana District, Tucutí, *Terry & Terry 1377* (F, not seen).

A. incarnata Leonard., Contr. U.S. Natl. Mus. 31: 242. 1958. TYPE: Colombia, *Haught 1315* (US).

Shrubs to 4 m high; stems subquadrangular in the younger portions, terete on the older portions, strigose to puberulous. *Leaves* oblanceolate to 28 cm long and 8 cm wide, glabrous above but strigose to pilose along the costa and the veins, glabrous to sparingly pilose beneath but strigose to pilose at the veins, apically acuminate and basally attenuate, the margins faintly crenate to entire; petioles to ca. 1 cm long, strigose to densely pilose. *Inflorescences* in terminal and subterminal spikes, the spikes to 12 cm long and 12 mm wide; rachis puberulous; bracts red, imbricate, obovate, to 10 mm long, 6 mm wide, lowermost bracts apically acute, other bracts obtuse and apiculate, the costa and the nerves prominent and deliquescent, the surface of the bracts with two sublateral clusters of orbicular, shiny glands at the midregion, 5–17 glands per cluster, the glands ca. 0.5 mm in diameter, surface of lowermost bracts strigose, upper bracts puberulous, the margins ciliate, densely so near the apex; bracteoles lanceolate, 5 mm

long, 1.5 mm wide, keeled, puberulous; peduncles to 6 cm long, mostly 1–2 cm long, strigose. *Flowers* with the calyx enclosed by a bract, the calyx 5-merous, all segments lanceolate, puberulous and prominently striate nerved, the anterior segments 6.5 mm long, 1.8 mm wide, the lateral segments 6 mm long, 1.2 mm wide, the posterior segment 7.5 mm long, 3 mm wide; corolla rose pink to red, bilabiate, the tube 4.5 cm long, 2.5 mm wide at base, 7 mm wide at the mouth, puberulous outside, glabrous inside, the upper lip erect, to 1.8 cm long, 9 mm wide, 2-lobed, the lobes lanceolate, 12 mm long, 5 mm wide at base, the apex acuminate and slightly keeled, the lower lip spreading, the middle lobe lanceolate, 23 mm long, 7.5 mm wide, keeled, acuminate, the lateral lobes triangular in free portion, attached on one side to the upper lip, acute, the free portion to 1.0 mm long, 1.0 mm wide at base; stamens exserted to just below the tip of the upper lip. *Capsules* clavate, about 2 cm long, 5 mm broad distally, 3 mm wide at base, glabrous and shiny, minutely punctate; seeds 4, suborbicular flattened, about 4 mm in diameter, 2 mm thick, surface minutely puberulous, reddish brown.

This species is found in rain forests of lower elevations and along streams and trails in Colombia and Panama.

CANAL ZONE: U.S. Army Tropic Test Center, Fort Clayton, 100–1000 ft, *Tyson et al. 3815* (DUKE). DARIÉN: Trail between Pinogana and Yaviza, ca. 15 m, *Allen 256* (MO). Río Pirre, near crossing of trail from El Real to Tucuti, *Duke* 5187 (MO). Hills near Piriaque, *Duke 8036, 8037* (both MO). Teotuma, 100 m, *Duke 10060* (MO). Río Pirre near town of Pirre, *Gentry & Clewell 6921, 6937* (both MO). Quebrada "Comachimuricate," cerca casa de Bartolo, *Kennedy 2832* (MO). Cerro Piraque, 100–1000 ft, *Tyson et al. 3851* (MO). SAN BLAS: Mainland opposite Achituppo, *Lewis et al. 126* (MO).

18. **Aphelandra tonduzii** Leonard, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1198. 1938. TYPE: Costa Rica, *Tonduz 13162* (US).

Herbs to 10 cm high; stems terete, pilose. *Leaves* elliptic to 24.5 cm long and 5 cm wide, pilose on both the surfaces, more densely so on the costa and the veins, apically acuminate, basally attenuate, the margins entire; petioles to 5.5 cm long, mostly 2–3 cm long, pilose. *Inflorescences* of loose axiliary spikes to 15.5 cm long, ca. 0.5 cm wide, the rachis subquadrangular, hirsute with numerous glandular hairs; peduncle subquadrangular, pilose; bracts lanceolate slightly keeled, to 7.5 mm long, 1.5 mm wide, puberulous with occasional glandular hairs, the margins ciliolate, occasionally with a pair of minute, marginal teeth, the bracts not imbricate at anthesis; bracteoles subulate, ca. 4.5 mm long, 0.6 mm wide, puberulous with occasional glandular hairs. *Flowers* with the calyx segments to 5 mm long, the posterior segment lanceolate, 1 mm wide, other segments subulate, 0.5 mm wide, all striate nerved, puberulous toward the tip; corolla white in bud, becoming purplish with age, bilabiate, the tube to 8 mm long, 1 mm wide at base, 1.5 mm wide at mouth, glabrous outside, puberulous within, the two lobes of the upper lip obovate, 2.5 mm long, 1 mm wide, the apex retuse, the middle lobe of the lower lip rhomboid obovate, 5 mm long, 5 mm wide, the apex retuse, the lateral lobes obovate, 4 mm long, 3 mm wide, apically retuse, minutely puberulous inside; stamens included, the filaments sparingly puberulous,

the anthers bearing a tuft of hairs at the apex. *Capsules* clavate, ca. 8 mm long, 3 mm broad at widest point, glabrous; seeds 4, obovate, flattened, 3 mm long, 2.5 mm wide, 1 mm thick, the surface hispidulous.

This species is found in rain forests at approximately 1,000 m in Costa Rica and Panama.

CHIRIQUÍ: Premontane oak rain forest between Pinola and Quebrada toward summit on Chiriquí Trail, *Kirkbride & Duke* 875 (MO).

2. ASYSTASIA

Asystasia Blume, Bijdr. 796. 1826. TYPE: *A. intrusa* (Forsk.) Blume.

Herbs or *shrubs*. *Leaves* with abundant cystoliths above when mature, entire, petiolate. *Inflorescences* of secund spikes or racemes, these loose or compact, simple or branched. *Flowers* solitary on short pedicels, subtended by 2 small bracts and 2 bractlets of about equal size; calyx 5-merous, the segments linear or lanceolate; corolla white, blue, purple, rose or yellow, the tube short to funnelform, the lobes subequal; stamens 4, didynamous, the anthers oblong with 2 parallel cells, sometimes spurred at the base; ovary 4-ovulate, pubescent; the stigma minutely 2-parted or subcapitate. *Capsule* elliptic, 2–4-seeded; seeds compressed, orbicular or irregularly angled, glabrous.

This genus is not native to the neotropics. According to Leonard (1951) about 70 species have been described, mostly from tropical Africa, Asia, and the East Indies.

1. **Asystasia gangetica** (L.) Anders. in Thwaites, Enum. Pl. Zeyl. 235. 1860.—FIG. 2.

Justicia gangetica L., Amoen. Acad. 4: 299. 1759. TYPE: India (not seen).

Herbs, ascending to ca. 30 cm; stems quadrangular, pilose. *Leaves* ovate to deltoid, to 5 cm long and 3.5 cm wide, apically acuminate, basally obtuse to truncate, both surfaces glabrate to sparingly pilose, especially on the veins, numerous cystoliths visible only on the upper surface, the margins crenulate to entire. *Inflorescences* in terminal, mostly secund racemes, to 16 cm long. *Flowers* on short pedicels ca. 2 mm long, yellow with purplish throats; 4 bractlets in 2 series subtending each flower, small, to 2 mm long, lanceolate, pilose; calyx and pedicel pilose and with numerous glandular hairs, the calyx lobes lanceolate, 5–7 mm long; corolla to 4 cm long, funnelform, the lower portion of the tube to 3.5 mm wide, 10 mm wide at the throat, the lobes semiorbiculate, ca. 10 mm wide, with numerous, minute, glandular hairs without, glabrous within; stamens 4, didynamous, included, the anthers 2-celled, each cell mucronulate both apically and basally, 3 mm long, 1 mm wide; ovary 3.5 mm long, the style velutinous 21 mm long, the stigma 2-lobed. *Capsule* oblong, to 13 mm long and 2 mm wide; seeds 2–4, flat, oval, ca. 1 mm long and 0.75 mm wide, oblique at the point of attachment, edged with dense mucilaginous hairs when wet.

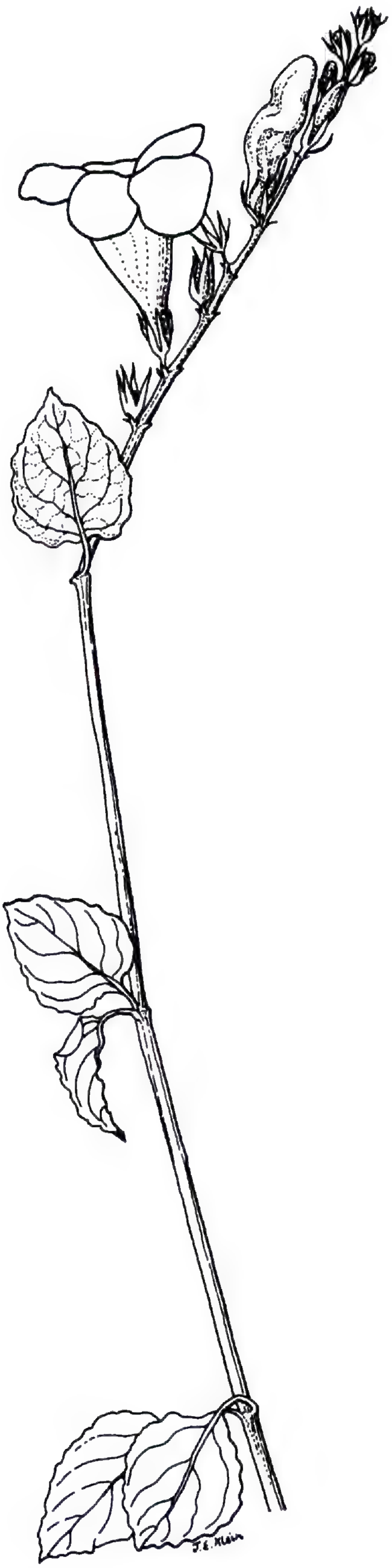

FIGURE 2. *Asystasia gangetica* (L.) Anders. Habit (×7/10). [After *D'Arcy 6720* (MO).]

This species is found in cultivation or as an escape in Panama and much of tropical America. It is native to tropical Africa, Asia and Malaya.

COCLÉ: Cultivated shrub, El Valle de Antón, *D'Arcy 6720* (MO). DARIÉN: El Real, weed in town, *Burch et al. 1061* (MO); *Durkee 71-121* (MO). PANAMÁ: Arraiján, *Rincón 307* (MO).

3. BARLERIA

Barleria L., Sp. Pl. 636. 1753; Gen. Pl., ed. 5. 283. 1754. TYPE: *B. prionitis* L.

Shrubs or *herbs*, erect, sometimes spiny. *Leaves* opposite, petiolate to nearly sessile, the cystoliths generally prominent and dense on both the surfaces, the margins entire. *Inflorescence* axillary or dense terminal bracted spikes. *Flowers* with the calyx deeply 4-lobed, the lobes unequal; corolla 5-merous, the broad, spreading lobes mostly subequal, bilabiate in Panama; stamens 4, didynamous, adnate to the base of the corolla tube, generally all stamens perfect, but American species with only 2 perfect stamens and 2 staminodes. *Capsules* ovate to oblong, flattened, with 2 seeds per locule; seeds flattened, ovate to suborbicular.

Over 100 species of this genus have been described, and nearly all of them occur in the Old World tropics.

1. **Barleria micans** Nees in Benth., Bot. Voy. Sulphur 146. 1844. TYPE: Panama (not seen).—FIG. 3.

B. discolor Nees in Benth., Bot. Voy. Sulphur 146. 1844. TYPE: Costa Rica (not seen).

Herbs; stems erect to 1.5 m, strigose, the hairs mostly 2-celled, appressed, to 1 mm long; cystoliths prominent and dense, to 3.3 mm long. *Leaves* lanceolate to oblanceolate, apically acuminate, basally attenuate, to 25 cm long and 7.5 cm wide, above sparsely strigose and with cystoliths many, beneath strigose and cystoliths few, the trichomes densest on the veins and the margins, bluish along costa upon drying; petioles to 4 cm long. *Inflorescences* in dense terminal spikes, cylindrical, to 7 cm long; bracts ovate, acuminate, basally acute, to 3.5 cm long and 1.5 cm wide, chartaceous, the costa prominent, the margins with spiny hairs to 2 mm long, sericeous inside, strigose outside plus with occasional glandular trichomes, the midvein and the base of each side velutinous, often bluish on drying; bracteoles 2, oblanceolate, to 2.0 cm long, ciliate, sericeous with simple and glandular trichomes. *Flowers* yellow, blue purple when dry, sessile; calyx segments unequal, the anterior segment elliptic, to 2.5 cm long and 1 cm wide, the apex bidentate, the margin with spines to 2 mm long, the lateral segments lanceolate, to 2 cm long and 2 mm wide, aristate apically, sericeous, the posterior segment slightly longer and narrower than the anterior segment, apically acuminate, the margins like the anterior segment; corolla bilabiate, the tube to 3 cm long, slender, 4 mm wide at the base, the lobes ca. 1.5 cm long, obovate, pilose; perfect stamens 2, the filaments glabrous, to 4 cm long, the anthers ca. 5 mm long, the imperfect stamens reduced to small staminodes ca. 0.2 mm long, each with a small centrally located spur; ovary pandurate, ca. 5 mm long, the style

FIGURE 3. *Barleria micans* Nees. Habit (×¼). [After *Busey* 388 (MO).]

4.2–4.5 cm long, glabrous, the stigma cylindrical to 1 mm long. *Capsules* elliptic, to 2 cm long, 1.6 cm wide, 2 mm thick, apically acuminate, dark purple brown when dry; seeds 4, velutinous and irregularly ovate, ca. 5 mm long, 0.3 mm thick.

This species is found along roadsides and trails, rain forests, and savannas.

CANAL ZONE: Chagres, ca. 4 km S of the river, *Busey* 388 (DUKE, MO). Madden Forest Road MR1, *Croat* 8927 (MO). Madden Dam, roadway leading downhill from the observation area adjacent to Dam, *Dwyer* 8395 (MO). Madden Forest Preserve, 75 m, *Hunter & Allen* 451 (MO); *Lewis et al.* 5319 (MO). CHIRIQUÍ: Burica Peninsula, Distrito Baru along ridge above Brazo Seco near Costa Rican border, 100–200 m, *Croat* 22545 (MO). COCLÉ: Mountains beyond La Pintada, 400–600 m, *Hunter & Allen* 635 (MO). PANAMÁ: Hills above

Campana, 600–800 m, *Allen 1690* (MO). Chiva-Chiva Road, 100 m, *Allen 4268* (MO). Between Chepo and El Llano, *Croat 14490* (MO). Between Río Pacora and Chepo, *Dwyer et al. 5112* (MO). LOS SANTOS: Tonosí, Guanico, 117 ft, *Stern et al. 1837* (MO). VERAGUAS: Trail between Cañazas and the foot of Cordillera Central, headwaters of Río Cañazas, 300–600 m, *Allen 179* (MO). PROVINCE UNKNOWN: *Cuming 1138* (MO).

4. BLECHUM

Blechum P. Br. ex Juss., Ann. Mus. Natl. Hist. Nat. 9: 269. 1807. TYPE: *B. brownei* Juss.

Perennial *herbs* or *shrubs*. *Leaves* lanceolate to ovate or cordate, apically acuminate or obtuse, basally attenuate, acute, obtuse or cordate, containing numerous cystoliths on both the surfaces, petiolate. *Inflorescences* in dense terminal spikes, the spikes squarrose; bracts single, imbricate, ovate oblong to ovate deltoid; bracteoles 2, oblanceolate to lanceolate. *Flowers* 5-merous, perfect; calyx segments slightly unequal, linear subulate; corolla white, blue, lavender, or purplish, funnelform with a narrow tube, the 5 lobes nearly equal; stamens 4, didynamous, the cells parallel and equal. *Capsules* oblong, flattened, dissepiment breaking away from the capsule wall at maturity; seeds few to 16, reddish brown, flattened, ca. 2 mm in diameter, the edges with a band of sticky dense mucilaginous hairs when wet, glabrous when dry.

The genus occurs mainly in tropical America, although species such as *B. pyramidatum* are reported from other tropical areas as well. Leonard (1951) stated that this genus consists of about 6 tenable species and that there is a close relationship between *Blechum* and *Ruellia*. *Blechum* can be recognized by its dense 4-sided spikes and very small flowers.

a. Leaf blades narrow, lanceolate or oblong lanceolate; mature leaves mostly under 15 mm wide ..... 2. *B. panamense*
aa. Leaf blades relatively broad, cordate, ovate or ovate lanceolate; mature leaves well over 15 mm wide.
  b. Corolla small, equalling or barely exceeding the bracts; bracts acute at the apex ..... 3. *B. pyramidatum*
  bb. Corolla relatively large, twice as long as the bracts or longer; bracts acuminate at the apex ..... 1. *B. costaricense*

1. **Blechum costaricense** Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1854: 168. 1855. TYPE: Costa Rica, *Oersted*, not seen.

B. dariense Lindau, Fedde Repert. Sp. Nov. 12: 423. 1913. TYPE: Panama, *Pittier 5549* (US).

Herbs, sometimes suffrutescent, to 1.3 m, the young stems quadrangular, pilose. *Leaves* ovate to ovate lanceolate, 3–10 cm long, 1.5–4.0 cm wide, apically acuminate, basally attenuate, the margins undulate, both the surfaces pilose to sparingly pilose and with numerous cystoliths. *Inflorescences* in terminal spikes, 4-sided, to 7 cm long; bracts ovate deltoid, apically cuspidate, basally rounded, to 2 cm long, 1.5 cm wide, the margins ciliate, sparingly pilose within and puberulent without; bracteoles 2, lanceolate, ca. 10 mm long, 2 mm wide. *Flowers*

2.0–2.5 cm long; calyx 5 mm long, the segments 0.5 mm wide at base, ciliate; corolla pale lavender to purple, extending well beyond the subtending bracts. *Capsule* oblong, flattened, ca. 8 mm long, puberulous.

This species is found in open woods, rain forests, along trails, riverbanks and shady cliffs and occurs in Costa Rica and Panama.

CANAL ZONE: Mojinga Swamp near mouth of Río Chagres, *Allen 868* (MO). Chagres, *Fendler 200* (MO). BARRO COLORADO ISLAND: *Croat 4193, 4288, 4292, 4355, 4365, 4541, 4923, 5751, 5779, 7300, 7317, 7445, 8017, 8085, 9242, 9413, 11904, 12226, 14054, 14068* (all MO); *Netting 15* (MO); *Robyns 65-16* (MO); *Shattuck 4, 141* (both MO); *Wetmore & Abbe 122* (MO); *Woodworth & Vestal 308* (MO). CHIRIQUÍ: Primary forest, 10–11 mi W of Puerto Armuelles near San Bartolo Limite, 300–500 m, *Croat 21981* (MO). Distrito Baru along ridge above Brazo Seco near Costa Rican border, 100–200 m, *Croat 22568* (MO). Burica Peninsula, disturbed area above Quebrada Yenbazales, 200 m, *Croat 22602* (MO). Rabo de Puerco, 8 km W of Puerto Armuelles, 50–150 m, *Liesner 40* (MO). Between Concepción and El Volcán, *White 310* (MO). DARIÉN: Quebrada "Comachimuricate" cerca casa de Bartolo, *Kennedy 2842* (MO). PANAMÁ: Cerro Jefe, *Dwyer & Gentry 9427* (MO). VERAGUAS: 5 mi W of Santa Fé on road past Escuela Agrícola de Alto Piedra on Pacific side of divide 800–1200 m, *Croat 23085* (MO).

2. **Blechum panamense** Lindau, Repert. Spec. Nov. Regni Veg. 12: 423. 1913. TYPE: Panama, *Pittier 2681* (MO).—FIG. 4.

Herbs to *subshrubs*; stems erect to 0.4 m, the younger stems sometimes sericeous in two lines. *Leaves* lanceolate, 3.0–11.5 cm long, the base narrowing to a very short-winged petiole, 0.5–1.8 cm wide, sparingly pilose to glabrous on both the surfaces, the margins entire. *Inflorescences* in loose to compact terminal spikes, to 4.5 cm long, the rachis puberulous to tomentose; bracts imbricate, ovate oblong, to 20 mm long and 5 mm wide, cuspidate at the apex, rounded at the base, pilose and sometimes puberulous, ciliate; bracteoles linear to 12 mm long and 1.5 mm wide, acuminate, pilose, ciliate. *Flowers* to 2.0 cm long, corolla tube to 1.0 cm long, extending beyond the subtending bract, lavender. *Capsule* oblong, flattened, ca. 6 mm long, puberulent.

This species is found along sandy and rocky river and stream banks.

BOCAS DEL TORO: Chiriquicito to 5 mi S along Río Guanumo, *Lewis et al. 2102* (MO). CANAL ZONE: Mojinga Swamp, *Allen 868* (MO). Quebrada Lopez at 30 m, *Allen 2136* (MO). Río Mendosa, 10 km N of Gamboa on Pipeline Road, 100 m, *Busey 326* (MO). Drowned forest of Quebrada Culebra, 70–75 m, *Dodge & Allen 17052* (MO). Río Indio, 70 m, *Dodge & Allen 17294* (MO). 6–8 mi N of Gamboa, *Gentry & Dwyer 3368* (MO). Pipeline Road, Río Agua Salud, *Kennedy et al. 3062* (MO). BARRO COLORADO ISLAND: *Croat 12339, 12340* (MO); Río Guanche 3 km upriver from road to Portobelo, 25 m, *Mori & Kallunki 5218* (MO).

3. **Blechum pyramidatum** (Lam.) Urb., Repert. Spec. Nov. Regni Veg. 15: 323. 1918.

Ruellia blechum L., Syst. Nat., ed. 10, 2: 1120. 1759. TYPE: not seen.
Barleria pyramidata Lam., Encycl. Méth. Bot. 1: 380. 1783. TYPE: not seen.
Blechum brownei Juss., Ann. Mus. Natl. Hist. Nat. 9: 270. 1807. TYPE: not seen.

Herbs; stems declining to erect, to 70 cm tall, the younger branches quadrangular, appressed puberulent. *Leaves* ovate to ovate lanceolate, 2–11 cm long,

FIGURE 4. *Blechum panamense* Lindau. Habit (×½). [After *Mori & Kallunki 5218* (MO).]

1–2.5 cm wide, both the surfaces sparsely pilose to glabrous plus numerous cystoliths which superficially resemble appressed hairs, the margins crenate to entire, apically acute, basally cuneate to obtuse. *Inflorescence* in terminal spikes, 4-sided, 1.5–7 cm long; bracts, ovate, 0.75–1.4 cm long, 0.6–1.1 cm wide, apically acute, basally rounded, ciliate, loosely strigose and densely puberulous; bracteoles lanceolate, 5 mm long, 1 mm wide, ciliate. *Flowers* 1.0–1.5 cm long, slightly longer than the subtending bract, white, pink, light blue, or purplish. *Capsule* oblong, flattened, ca. 6 mm long, puberulent; seeds 16.

This species is found in disturbed areas, riverbanks, roadsides, lawns, pastures, and low areas. It occurs in eastern and southern Mexico, Central America, the West Indies, South America, and also in Guam, Formosa, and the Philippine and Caroline Islands.

BOCAS DEL TORO: Shepard Island, Chiriquí Lagoon, *Wedel 2709* (MO). Nievecita, 0–50 m, *Woodson et al. 1856* (MO). CANAL ZONE: Near mouth of Río Chagres, *Allen 868* (MO). Near mouth of Río Chagres, *Allen 878* (MO). Ft. Clayton, *Correa 780* (MO). Albrook Air Base, Army Tropic Test Center site, *Dwyer & Robyns 128* (MO). Chagres, *Fendler 225* (MO). Outskirts of Ancón, *Greenman & Greenman 5079* (MO). Las Cruces Trail, 75 m, *Hunter & Allen 709* (MO). ½ mi S of Gamboa along Chagres River, *Lazor 2278* (MO). Along road, *Lewis et al. 5180* (MO). Roadside ½ mi NW of Gamboa, ca. 70 m, *Liesner 1398* (MO). Boy Scout Road, Madden Dam area, *Porter et al. 4059* (MO). Near Madden Dam, *Steyermark* (MO). BARRO COLORADO ISLAND: *Croat 4567, 4604, 5795, 6924, 6925a, 6953, 6966, 7088, 7245, 8825, 9160* (all MO); *Ebinger 203* (MO); *Netting S* (MO); *Robyns 65-16, 65-17* (both MO); *Shattuck 537* (MO). CHIRIQUÍ: 10–11 mi W of Puerto Armuelles, San Bartolo Limite, 300–500 m, *Croat 21991A* (MO). Quebrada Quanabanito beyond La Repressa, 2 mi SW of Puerto Armuelles, 0–200 m, *Croat 22070* (MO). Ridge above Brazo Seco near Costa Rican border, 100–200 m, *Croat 22559* (MO). David Airport, 25 ft, *Lewis et al. 735* (MO). COCLÉ: 3 mi NE of Antón, *Croat 9613* (MO). 10 mi E of Nata at Río Grande, *Tyson 5285* (MO). DARIÉN: Santa Fé, *Duke 9482* (MO). Hydro Camp Río Pendejo on Río Sabana, 50 ft, *Duke 15430* (MO). HERRERA: ½ mi NE of Ocú, *Stern et al. 1702* (MO). LOS SANTOS: 7 mi S of Chitré, *Croat 9709* (MO). Ca. 7 mi S of Chitré, *D'Arcy & Croat 4181* (MO). 11 mi N of Tonosí, *Dwyer 2959* (MO). Tonosí, road between Tonosí and Guánico, *Stern et al.* (MO). PANAMÁ: Taboga Island to 300 m, *Allen 104* (MO). Río Pita, 1–3 mi above confluence with Río Maestra, *Duke 4754* (MO). Isla del Rey, *Duke 9535* (MO). Cermeno, *Dwyer 6620* (MO). Between Río Pacora and Chepo, *Dwyer et al. 5100* (MO). Cerro Campana, *Lewis et al. 3065* (MO). W of Chepo, *Tyson 5364* (MO). SAN BLAS: Near Puerto Obaldía, *Croat 16961* (MO).

5. BRAVAISIA

Bravaisia DC., Rev. Bignon. in Bibl. Univ. Genève Ser. 2 17: 117–136. 1838. TYPE: *B. floribunda* DC.

Shrubs or *trees*. *Leaves* ovate to ovate elliptic, apically acute to acuminate, petiolate, the margins entire to slightly undulate. *Inflorescences* terminal in compact leafy panicles. *Flowers* subtended by a pair of bracts; calyx 5-merous, subcoriaceous; corolla white, yellow or purplish with a short tube and campanulate throat, 5-lobed, subequal; stamens 4, the anther cells 2, contiguous, spurred at the base. *Capsules* with 4–8 seeds.

Five species are found in Mexico, Central America, Colombia, Venezuela, and the West Indies.

1. **Bravaisia integerrima** (Spreng.) Standley, Contr. U.S. Natl. Herb. 23: 1335. 1926.—FIG. 5.

Amasonia integerrima Spreng., Syst. Veg. 2: 765. 1825. TYPE: Colombia, *Bertero* (G, not seen).

Onychacanthus speciosus Oerst., Viderst. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1854: 131. 1854. TYPE: Costa Rica, *Oersted* (not seen).

Tree to 18 m high; branchlets quadrangular, glabrous to puberulous or tomentose on the youngest portions. *Leaves* ovate to ovate elliptic, to 28 cm long, 10 cm wide, apically acute or acuminate, basally acute or oblique, the margins entire to slightly undulate, subcoriaceous, the surfaces glabrous, the costa and the lateral veins slightly pilose; petioles ca. 3 cm long. *Inflorescence* terminal in compact leafy panicles, to 13 cm long, 25 cm wide, the peduncles quadrangular; flowers subtended by 2 oval bractlets 2 mm long, apically obtuse, ciliolate and puberulent. *Flowers* with the corollas white or yellow with a purple spot in the throat, 1.5–2.0 cm long, glabrous, the tube campanulate, ca. 8 mm wide at the throat, the limb ca. 2 cm across, the lobes ca. 1 cm long, 6–8 mm wide, rounded or emarginate. *Capsule* elliptic, flattened, 10–12 mm long, glabrous, 8-seeded.

This species is found in low wet woods and meadows in Peru, Colombia, Venezuela, and north to Oaxaca and Tamaulipas in Mexico.

According to Leonard (1951) this tree often has masses of aerial roots similar to those of mangroves. He also reports that the wood is medium heavy and suitable for packing-boxes and food pails.

BOCAS DEL TORO: Region of Almirante, *Cooper & Slater 25* (US); *Cooper 25a* (MO). CHIRIQUÍ: Quebrada Manzanillo, 9 km S × SW of Puerto Armuelles, *Busey 724* (MO). Progreso, *Cooper & Slater 269* (US). Primary forest and forest edge, Rabo de Puerco, 8 km W of Puerto Armuelles, 50–150 m, *Croat 21966* (DUKE, MO). Quebrada Quanabanito beyond La Repressa 2 mi SW of Puerto Armuelles, 0–200 m, *Croat 22079* (MO). Burica Peninsula, Quebrada Caña Blanca, 40 m, *Croat 22579* (MO).

6. CHAETOCHLAMYS

Chaetoclamys Lindau, Bull. Herb. Boissier 3: 490. 1895. LECTOTYPE: *C. macrosiphon* Lindau.

Herbs or suffrutescent plants. *Leaves* ovate to lanceolate. *Flowers* borne in short spikes which are crowded into a terminal, congested head; bracts and bracteoles narrow. *Flowers* with the calyx segments 5, narrow; corolla salverform, bilabiate, the upper lip 2-lobed, the lower lip 3-lobed; stamens 2, exserted, the cells attached at different heights, the lobe spurred. *Capsules* clavate; seeds 4.

All of the 14 species described for this genus are from tropical America.

1. **Chaetochlamys panamensis** Lindau, Fedde Rep. Spec. Nov. 11: 124. 1912. SYNTYPES: Panama, *Pittier 2338, 2614* (B, not seen).—FIG. 6.

Herbs to 50 cm tall; stems branching, erect or decumbent, sometimes rooting at lower nodes, terete, glabrous to puberulous along two lines. *Leaves* lanceolate elliptic, to 8.5 cm long, 2.8 cm wide, apically acuminate, basally attenuate,

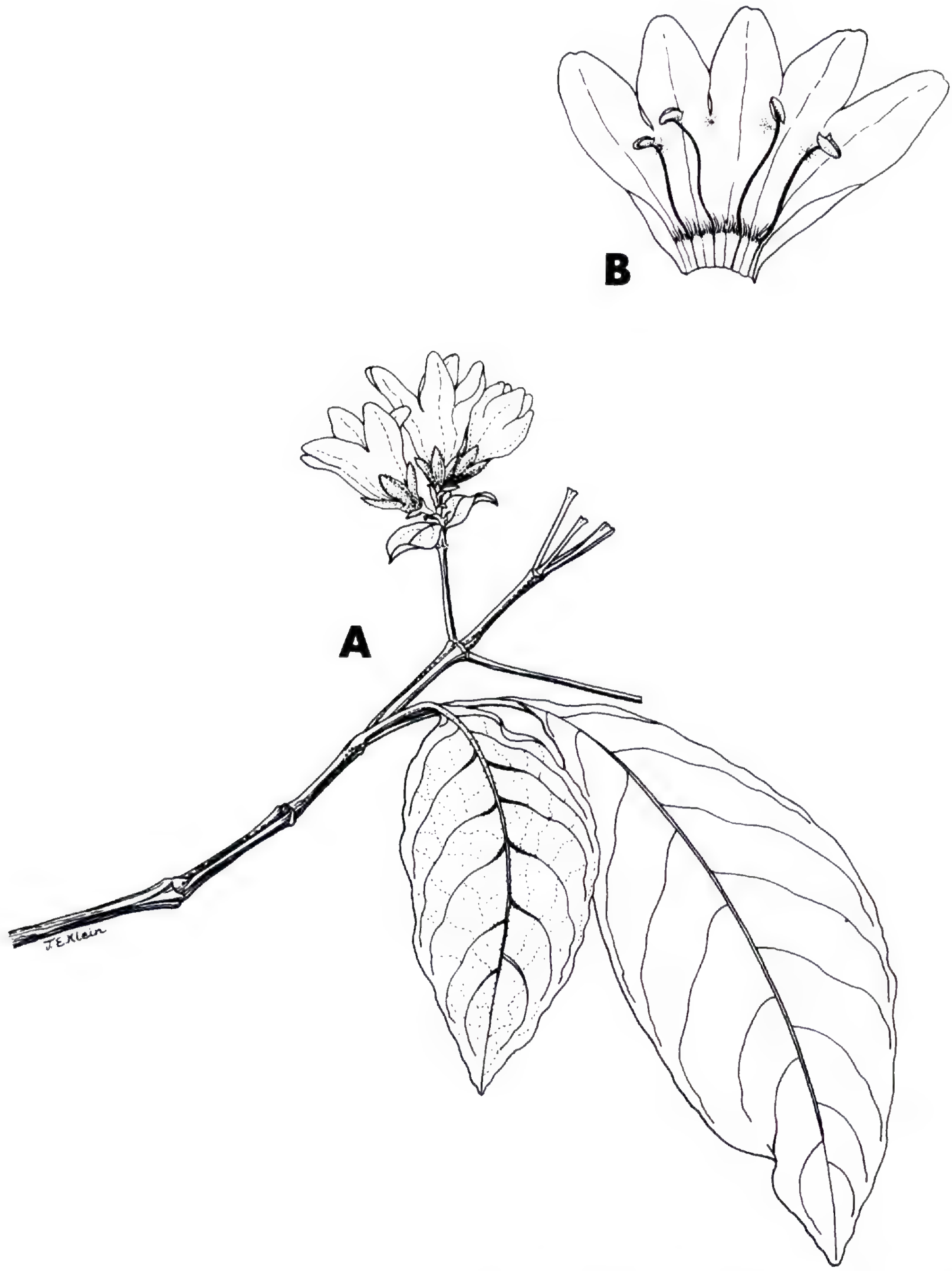

FIGURE 5. *Bravaisia integerrima* (Spreng.) Standley.—A. Habit (×⅘).—B. Opened flower (×1⅗). [After *Croat 21966* (MO).]

glabrous to sparingly puberulous along the costa and the veins, the cystoliths dense, prominent on both surfaces, the margins entire to undulate; petioles to 1 cm long, puberulous to glabrous. *Inflorescences* in terminal heads; bracts linear to 22 mm long, 0.75 mm wide, ciliate, the hairs to 1.5 mm long; bracteoles similar

FIGURE 6. *Chaetochlamys panamensis* Lindau. Habit ($\times 9/10$). [After *Tyson et al.* 2945 (MO).]

but shorter and narrower. *Flowers* sessile; calyx segments lanceolate, 10 mm long, 1.5 mm wide, ciliate; corolla pink or purplish, sparingly glandular puberulous, to ca. 4 cm long, the tube ca. 22 mm long, 4 mm broad, the upper lip oblong, 10 mm long, 3 mm wide, apically bilobed, the middle lobe orbicular, 10 mm in diameter, the lateral lobes elliptic, 12 mm long, 8 mm wide; stamens exserted to just above the mouth, the filaments glabrous, ca. 5 mm long, attached just beneath the mouth, the anther cells unequal, inserted at different heights, the upper cell 2 mm long, basally acute, the lower cell 2.5 mm long, basally sub-

calcarate, the connective ca. 1 mm wide. *Capsules* stout clavate, to 12 mm long, 4.5 mm wide, 3 mm thick, glabrous; seeds 4, suborbicular, not flattened, ca. 2 mm in diameter, glabrous.

CANAL ZONE: Drowned forest of Quebrada Bonita, 70–80 m, *Dodge & Allen 17069* (MO). Along banks of Río Indio, 70–100 m, *Dodge & Allen 17372* (MO). Madden Dam, *Dwyer 8370* (MO). Madden Dam, 50 ft, *Lewis et al. 24* (MO). Río Cocoli, Road K-9, *Stern et al. 335* (MO). Drowned forest of Quebrada Bonita and along its branches, 70–80 m, *Steyermark & Allen 17156* (MO). Drowned forest and sabanas on banks of Quebrada Melgada, Casa Larga Trail, 70–75 m, *Steyermark 17478* (MO). CHIRIQUÍ: Cerro Vaca, 900–1136 m, *Pittier 5330* (US). COLÓN: Juan Mina plantation, Río Chagres, above Gamboa, 25 m, *Allen 4143* (MO). HERRERA: Ocú 100 m, *Allen 4077* (MO). Road from La Avena to outskirts of Pesé, 200 ft, *Burch et al. 1296* (MO). LOS SANTOS: Road between Tonosí and Macaracas, *Oliver et al. 3554* (MO). 10 mi N of Tonosí, *Tyson et al. 2945, 2946* (both MO). 12 mi S of Macaracas, *Tyson et al. 3072* (MO). PANAMÁ: Río Tocumen, N of Chepo road, to 30 m, *Hunter & Allen 243* (MO, US). Sabanas N of Panama City, *Paul 462* (US). Dry wooded hills around Alhajuela, 30–100 m, *Pittier 2338* (US). Agricultural Experiment Station at Matias Hernández, *Pittier 6878* (US). Río Tapia, wet forest, *Standley 26145, 28039, 29331, 41185* (all US). VERAGUAS: 1 mi W of Santiago along old Interamerican Highway, *Tyson 5184* (MO). Puerto Mutis, 12 mi S of Santiago, *Tyson 5196* (DUKE, MO). PROVINCE UNKNOWN: Banks of lower Río Calra, *Maurice 792* (US).

7. CHAETOTHYLAX

Chaetothylax Nees in Mart., Fl. Bras. 9: 153, *pl. 26*. 1847. TYPE: *C. tocatinus* Nees.

Herbs. *Leaves* ovate to elliptic. *Inflorescences* with flowers more or less secund, in short, dense, terminal and axillary spikes which often form panicles; bracts narrow with filiform tips, puberulous with ciliate margins. *Flowers* with the calyx 4-merous, the segments resembling the bracts; corollas white or purplish, puberulous, bilabiate, the lips subequal, the upper lip narrowly ovate, the lower lip deeply 3-lobed, the lobes rounded; stamens slightly exserted, not exceeding the corolla lips, the anthers 2-celled, the upper cell oblong, the lower cell reduced, vestigial, or hairlike, the lobes separated by a slender filiform connective. *Capsules* clavate; seeds 4, papillose or puberulous.

Eight species occur in Central and South America. Superficially this genus can be confused with the genus *Chaetochlamys*, but it is distinguished from that genus by its smaller flowers and capsules and its 4-merous calyx.

1. **Chaetothylax leucanthus** Leonard, Contr. U.S. Natl. Herb. 31: 664. 1958. TYPE: Colombia, *Pennell 3985* (NY, not seen).—FIG. 7.

Herbs to 60 cm tall; stems erect, terete, with retrorse hairs mostly along two lines. *Leaves* ovate elliptic to elliptic, to 8 cm long, 3 cm wide, apically acute, cuspidate at the tip, basally attenuate, glabrous above, sparingly strigose beneath, the hairs more dense on the costa and the veins, the cystoliths dense and prominent above, the margins entire to crenate; petioles short, to ca. 5 mm long, strigose. *Inflorescences* in compact terminal and axillary spicate panicles, the spikes to 4 cm long, 1 cm wide, dense, more or less one-sided; panicles subtended by small leaves; bracts narrowly subulate, to 9 mm long, 0.5 mm wide, ciliate, and moderately puberulous. *Flowers* with 4-merous calyx, segments narrowly subulate,

FIGURE 7. *Chaetothylax leucanthus* Leonard. Habit (×9/10). [After *Croat 8966* (MO).]

to 11 mm long, ca. 0.4 mm wide, ciliate and minutely glandular puberulous; corolla white, ca. 14 mm long, puberulous except at the base, the tube cylindrical, 9 mm long, 0.5 mm in diameter, the upper lip ovate oblong, 3.5 mm long, 1 mm wide, apically emarginate, the lower lip 3-lobed, ca. 3.25 mm long, the lobes oblong, 2 mm long, the middle lobe 1.5 mm wide, the lateral lobes 1.25 mm wide, all apically obtuse; stamens exserted about half the length of the upper lip, the upper anther cell 0.75 mm long, the lower cell attached 0.5 mm beneath the upper cell, reduced, sterile, the filaments glabrous. *Capsule* clavate, 6 mm long, 1 mm broad, 2 mm thick, puberulous; seeds 4, orbicular, slightly flattened, 1 mm in diameter, 0.5 mm thick, puberulous.

This species is found along trails and in clearings at lower elevations.

CANAL ZONE: Boy Scout Road near path to lake, *Croat 8966* (MO). Boy Scout Road, Madden Dam area, second growth forest, *Porter et al. 4037* (MO). PANAMÁ: Cermeño, *Dwyer & Robyns 98* (MO).

8. DICLIPTERA

Dicliptera Juss., Ann. Mus. Hist. Nat. Paris 9: 267. 1807, nom. cons., not *Diapedium* Konig. (1805). TYPE: *D. chinensis* (L.) Juss., typ. cons.

Herbs or *shrubs*; stems more or less hexagonal in cross section. *Leaves* mostly ovate with entire or undulate margins, petiolate. *Inflorescences* of cymes, spikes, panicles or thyrses, subtended by 2–4 pairs of conspicuous involucrate bracts. *Flowers* with the calyx 5-merous, hyaline; corollas narrow, slightly funnelform, bilabiate; stamens 2, the anther cells often unequal; staminodes absent. *Capsules* ovate or clavate; seeds 2 or 4.

There have been 150 species of the New and Old World tropics and subtropics described for this genus, most easily recognized by its hexagonal stems and flattened reduced cymes with bracts.

a. Inflorescences in axillary cymes; corollas 3 cm long or more.
  b. Floral bracts rounded and apiculate.
    c. Leaf bases obtuse to rounded; corolla bright pink ..... 1. *D. gracilis*
    cc. Leaf bases attenuate; corolla purplish ..... 4. *D. trifurca*
  bb. Floral bracts apically acute ..... 3. *D. iopus*
aa. Inflorescences in terminal spicate panicles or terminal and axillary spikelike thyrses; corollas 2.5 cm long or less.
  d. Inflorescences in spikelike thyrses (narrow, compact panicles with cymose lateral branches); corollas white ..... 2. *D. imbricata*
  dd. Inflorescences in spicate panicles (clusters of spikes); corollas red .. 5. *D. vahliana*

1. **Dicliptera gracilis** Leonard, Ann. Missouri Bot. Gard. 28: 467, *fig. 2.* 1941. TYPE: Panama, *Woodson & Schery 569* (MO).

Herb to 30 cm tall; stem erect, glabrous to sparingly puberulous. *Leaves* ovate lanceolate, 2–3.5 cm long, 1–1.5 cm wide, apically acuminate, basally obtuse to rounded, glabrous, the cystoliths present but inconspicuous, the margins entire; petioles ca. 3 mm long, glabrous. *Inflorescences* in axillary cymes of 3 flowers each; peduncles to 4 cm long, sparingly puberulous; bracts subtending the cymes, leaflike, frequently exceeding the calyx; floral bracts oblong, unequal, the larger

ones to 9 mm long, 1 mm wide, the shorter ones, 5 mm long, 1 mm wide, all apically obtuse or rounded and also apiculate, the margins ciliolate; bractlets lanceolate, 4 mm long, 1 mm wide, sparingly puberulous toward the apex; pedicles to 3 mm long, puberulous. *Flowers* with the corolla bright pink, 3 cm long, densely puberulous, the tube ca. 10 mm long, 1 mm broad basally, expanding to 3 mm broad at the mouth, the lips ca. 20 mm long; stamens exserted to about the tips of the lips, the filaments puberulous, the anther cells equal and parallel, 2 mm long, basally rounded and apiculate. *Capsules* not observed.

This species is most similar to *D. trifurca* and differs from it mainly in its small size, smaller leaves, and its basally obtuse or rounded leaves.

CHIRIQUÍ: Vic. of Bajo Mona and Quebrada Chiquero, 1500 m, *Woodson & Schery* 569 (MO).

2. **Dicliptera imbricata** Leonard, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1210. 1938. TYPE: Costa Rica, *Brenes 21440* (US, not seen).

Herb to 1 m tall; stems branched, sometimes rooting at the lower nodes, puberulous mostly at the angles in the younger portions, basal portions terete and glabrous. *Leaves* elliptic, to 9 cm long, 3 cm wide, apically acuminate, basally attenuate, glabrous to sparingly puberulous along the costa and the veins, the cystoliths dense and prominent on both surfaces, the margins entire; petioles to 1.5 cm long, puberulous. *Inflorescences* in terminal and axillary spikelike thyrses, to 4 cm long, 2 cm wide, cymes 2, fanlike, of 3–5 flowers each at every node, each cyme subtended by a pair of oblong-lanceolate bracts 3–8 mm long, 0.5–1 mm wide, puberulous; bracts subtending the flowers unequal, obovate, to 7 mm long, 3.5 mm wide, whitish basally, greenish apically, strongly 3-nerved, puberulous with ciliate margins; outer pair of bracteoles linear, slightly falcate, 5 mm long, 0.75 mm wide, apically acuminate, ciliate, the inner bracteoles lanceolate, 4 mm long, 0.5 mm wide, ciliolate. *Flowers* with the calyx segments linear subulate, 3 mm long, 0.25 mm wide, minutely puberulous; corolla white, lavender striped, to 16 mm long, puberulous, the tube cylindrical, 10 mm long, 1 mm wide, the lips oblong, 6 mm long, 2 mm wide, apically minutely dentate; stamens exserted to near the tips of the lips, the filaments ca. 5 mm long, puberulous, the anther cells superposed, basally obtuse. *Capsules* elliptic, ca. 4 mm long, 1 mm wide, puberulous toward the tip; seeds 2, oval, flattened, ca. 1 mm long, roughened.

This species is found along trails in rain forest at elevations to ca. 1,000 m in Costa Rica and Panama.

COCLÉ: N rim of El Valle de Antón, 600–1000 m, *Allen 1665* (F, MO, NY, US). VERAGUAS: 16 km NW of Santa Fé, on road to Calovébora (Panama Highway 35), 300–500 m, *Mori & Kallunki 6098* (MO).

3. **Dicliptera iopus** Lindau, Pittier, Primit. Fl. Costaric. 2: 305. 1900. TYPE: Costa Rica, *Tonduz 2136* (B?, not seen).—FIG. 8.

Shrub to 3.5 m tall; stems strigose to glabrous. *Leaves* ovate to elliptic, to 16 cm long, 6.5 cm wide, often smaller, apically acuminate, basally acute, glabrous

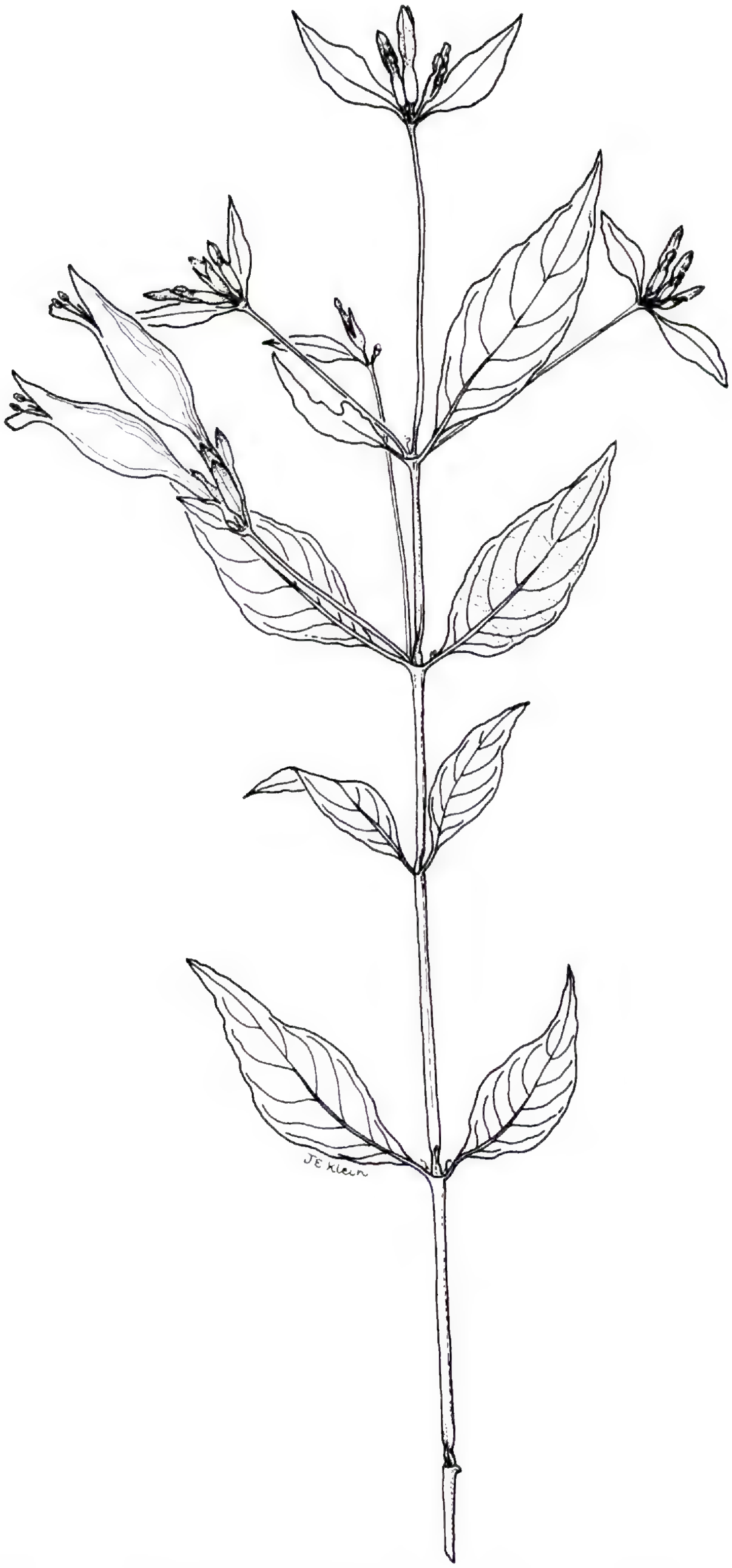

FIGURE 8. *Dicliptera iopus* Lindau. Habit (×7/10). [After *Woodson & Schery 616* (MO).]

to sparingly strigose on both surfaces, the margins entire, the petioles variable to 7 cm long, glabrous to sparingly puberulous. *Inflorescences* in axillary cymes, each cyme subtended by 2 elliptic to ovate-oblong bracts, to ca. 3 cm long, 1 cm wide, apically acute, basally acute, glabrous to sparingly pilosulous; bracts 2, unequal, subtending each flower, both linear oblong, fused at the base, the longer bract 10–16 mm long, 4 mm wide at the base, the shorter bract to 12 mm long, 4 mm wide, both bracts apically acute, keeled, sparingly puberulous on both surfaces; bractlets 4, the outer pair oblanceolate, to 8 mm long, 2 mm wide, puberulous toward the tip, the inner pair smaller, 3.5 mm long, 0.5 mm wide; peduncles to ca. 6.5 cm long, subhexangular, puberulous along the ridges, the pedicels (2)3(4), the middle one longest, to ca. 4 mm long, sparingly puberulous; usually 3 per cyme. *Flowers* with the calyx 5-merous, coalesced for ½ of its length, to 7 mm long, the lobes linear, ca. 3.5 mm long, subtomentose; corolla lavender, inflated at about the middle of the tube, bilabiate, the tube to 4 cm long, 2.5 mm wide at the base, 8 mm wide at the mouth, glandular puberulous both inside and out, the upper lip entire, acute, ca. 9 mm long, 5 mm wide, the lower lip ca. 11 mm long, 8 mm broad at the base with 3 small, suborbiculate lobes at its apex, ca. 0.5 mm long; stamens exserted, the filaments flattened, pilose, the anther cells equal; style exserted, glabrous. *Capsule* clavate, ca. 15 mm long, apiculate, densely glandular puberulous; seeds 2 per capsule, flattened, suborbicular, ca. 3 mm in diameter.

This species is found in dense shade of rain forests in Costa Rica and Panama.

BOCAS DEL TORO: Robalo trail, N slopes Cerro Horqueta, 6000–7000 ft, *Allen 4994* (MO). CHIRIQUÍ: "New Switzerland," central valley of Río Chiriquí Viejo, 1800–2000 m, *Allen 1363* (MO). Bajo Mono-Robalo trail, W slopes of Cerro Horqueta, 5000–7000 ft, *Allen 4810* (MO). Between Bambito and Cerro Punta, *Croat 10587* (MO). Methodist Camp near Nueva Swissa, *Croat 13505* (MO). Palo Santo, 3 mi N of Volcán, *Croat 13564* (MO). Bajo Corro, 6000 ft, *Davidson 65* (MO). Valley of Río Chiriquí Viejo N Volcán City, 5200–5600 ft, *Duke 9044* (DUKE, MO). Along Boquete Trail, Cerro Respinga, 2000–2500 m, E of Town of Cerro Punta, *Gentry 5921* (MO). Premontane rain forest between Pinola and Quebrada Hondo toward summit on Chiriquí trail, *Kirkbride & Duke 874* (MO). Cerro Punta, 2.5 mi S of Florida State University Tropical Biology Station, 5500 ft, *Sawyer* (MO). Valley of Río Chiriquí Viejo N of Volcán City, 5200–5600 ft, *White 18, 176* (both MO). Bajo Chorro, 1900 m, *Woodson & Schery 616* (MO). Between Bambito and Cerro Punta, *Wilbur et al. 10962* (DUKE). Bajo Chorro, 1900 m, *Woodson & Schery 616* (MO).

4. **Dicliptera trifurca** Oerst., Vidensk. Meddel.-Dansk Naturhist. Foren. Kjøbenhavn 1854: 172. 1855. TYPE: Costa Rica *Oersted*, not seen.

D. trifurcata (Oerst.) Hemsl., Biol. Centr. Amer., Bot. 2: 525. 1881.
Dipedium trifurcatum (Oerst.) Kuntze., Rev. Gen. Pl. 2: 485. 1891.

Herbs, sometimes suffrutescent, to 2 m tall; stems branching, glabrous. *Leaves* ovate elliptic, to 12 cm long, 4 cm wide, apically acuminate, basally attenuate, glabrous to sparingly puberulous along the costa and the veins beneath, the cystoliths more prominent beneath, the margins undulate; petioles to 3.5 cm long, glabrous to sparingly puberulous along 2 lines. *Inflorescences* in axillary cymes of 3 flowers each; peduncles to 8 cm long, mostly glabrous; bracts subtending the cymes, leaflike, frequently exceeding the calyx; floral bracts oblong to oblong spatulate, unequal, the larger one to 11 mm long, 2 mm wide, the smaller

one to 7 mm long, 1.5 mm wide, both apically rounded and apiculate, glabrous; bractlets oblong lanceolate, to 5 mm long, 1 mm wide, sparingly puberulous; pedicels to 3 mm long, glabrous to sparingly puberulous. *Flowers* with the calyx 5-merous, 6 mm long, the segments subulate, 4 mm long, 0.6 mm wide, puberulous; corolla red violet or purplish, 3.5–5.5 cm long, puberulous, the tube to 4 cm long, 2 mm broad basally, expanding to 7 mm wide at the mouth, the lips oblong to ca. 1.5 cm long, the upper lip 7 mm wide, apically acute, lower lip 3-lobed, the lobes subequal, ca. 0.75 mm long; stamens exserted to the tip of the upper lip, the filaments sparingly puberulous, the anther cells parallel, ca. 3 mm long, basally apiculate. *Capsules* stipitate, to 18 mm long, 4 mm wide, 2 mm thick, puberulous; seeds 4, flattened, suborbicular, ca. 4 mm in diameter, papillose.

This species is found in rain forests in Costa Rica and adjacent Panama at elevations above 1,000 m.

CHIRIQUÍ: Primary forest and adjacent cutover area, Las Nubes, 2.7 mi NW of Río Chiriquí Viejo W of Cerro Punta, 2200 m, *Croat 22370* (MO). On slope of La Popa above Boquete, 5400 ft, *D'Arcy & D'Arcy 6374* (MO). Bajo Chorro, Boquete District, *Davidson 65* (F). Cerro Punta, 2.5 mi S of Florida State University Tropical Biology Station, 5500 ft, *Kozlovsky K-4* (MO). Side of Sierra del Boquete, 1380 m, *Maurice 741* (MO, US). Cerro Punta, 2.5 km SE of town, *Mori & Kallunki 5652* (MO). Trail through the Paseo de Respinga on way to Boquete, ca. 7500 ft, *Wilbur & Teeri 13177* (DUKE). Heavily forested slopes above the Río Caldera beyond Bajo Mano, 1800 m, *Wilbur et al. 11058* (DUKE).

5. **Dicliptera vahliana** Nees in DC., Prodr. 11: 489. 1847. LECTOTYPE: Colombia, *Bertero*, not seen.

Herbs to 1.5 m tall; stems hexagonal with ridges at the angles, glandular puberulous along the ridges. *Leaves* lanceolate to 9 cm long, 3.5 cm wide, apically acuminate, basally acute, the major costa relatively prominent on both surfaces, pilose above and beneath, the margins entire, the petioles ca. 7 mm long, puberulous. *Inflorescences* in lax spikes forming much branched terminal panicles, the rachis and the peduncles with minute disc-tipped glandular hairs, the branches of the panicles subtended by a pair of subulate bracts 1–1.5 mm long, 0.6–1 mm wide at the base; each flower subtended by 6 involucral bracts, outermost 2 spathulate, ca. 5 mm long, 1 mm wide at the base, 4 inner bracts subulate, ca. 2 mm long, 0.5 mm wide at base, all the bracts glandular puberulous and with subhyaline margins; flowers mostly sessile and borne singly, but occasionally in fascicles of 2 or 3 and subsessile. *Flowers* with the calyx 5-merous, 2 mm long, fused about ½ its length, the segments subulate, 1 mm long, ciliolate; corolla red, bilabiate, to 2.5 cm long, 5 mm wide at the mouth, 1 mm wide at the base, puberulous, the lips each ca. 1.5 cm long, 6 mm wide at the base, the upper lip erect, rounded at the tip, the lower lip recurved, 3-lobed at the tip, the lobes ca. 0.75 mm long, the middle lobe 0.5 mm wide, the lateral lobes slightly narrower, all rounded; stamens exserted, extending nearly to the tip of the upper lip of the corolla, the filaments adnate to the corolla tube for ca. 15 mm, pilosulous, the anthers oblong 2.6 mm long, 1.5 mm wide. *Capsules* clavate, flattened, to 7 mm long, 2.5 mm wide at widest point and ca. 0.5 mm thick; seeds 2, suborbicular, flattened, ca. 1.5 mm in diameter, with numerous flat-tipped glandular hairs.

Found in moist, sandy and often saline soil of disturbed areas such as pastures and meadows, this species occurs in southern Florida, the West Indies, Panama and northern South America.

CANAL ZONE: Victoria Fill near Miraflores Locks, *Allen 1705* (MO). Boy Scout Road near path to lake, *Croat 8965* (MO). Railroad and dockyards at Balboa, *Macbride & Featherstone 23* (F). Between Corozal and Ancón, 10–30 m, *Pittier 2645* (US). Boy Scout Road, Madden Dam area, second growth forest, *Porter et al. 4033* (MO). Balboa, *Standley 32107* (US). Chiva-Chiva Trail 1 mi W of Miraflores Lake, *Tyson & Blum 3567* (MO). CHIRIQUÍ: Burica Peninsula, Quebrada Melliza, 6 mi S of Puerto Armuelles, 0–150 m, *Liesner 470* (MO). COLÓN: On rocky shoreline, Garotte, ca. 10 km SE of Portobelo, *D'Arcy 4006* (MO). DARIÉN: Isla Pedro Gonzales, *Duke 10408* (US). LOS SANTOS: Salinas de Chitre, *D'Arcy 4196A* (MO). PANAMÁ: Isla Chepillo, *Duke 10327* (US). Isla del Rey opposite Isla Espiritu Santo, *Duke 10469* (DUKE). Panama, *Macbride 2605* (F, US). Taboquilla Island at edge of clearing, *Miller 2007* (US). Sabanas N of Panama City, *Paul 406* (US). El Capitano, 4 mi E of Chepo, roadside ditch, *Tyson 5361* (DUKE, MO).

9. DYSCHORISTE

Dyschoriste Nees in Wallich, Pl. Asiat. Rariores 3: 75, 81. 1832. TYPE: *D. depressa* Nees = *D. erecta* (Burm.) O. Kuntze.

Calophanes D. Don in Sweet, Brit. Fl. Gard. 2: *pl. 181.* 1833. TYPE: *C. oblongifolia* (Michaux) D. Don.

Herbs to suffrutescent shrubs. *Stems* prostrate, ascending or erect, glabrous or pubescent. *Leaves* sessile or petioled, mostly entire. *Inflorescence* cymose, capitate, or spicate, terminal or axillary. *Flowers* subtended by foliaceous bracts and bracteoles; calyx deeply 5-parted, usually subulate setaceous, ciliate; corolla 5-merous, obscurely or distinctly bilabiate, the tube erect, the limb spreading; stamens 4, didynamous, the anthers 2-celled, the cells oblong, minutely calcarate to mucronate at the base. *Capsule* included in the persistent calyx, oblong linear, glabrous, separating with difficulty at maturity into 2 valves; seeds 2–4, flattened, suborbicular, with mucilaginous hairs when wet.

A widely distributed genus in both tropical and subtropical regions of the world, although a few species are found in warm temperate areas. Several species occur in Central America.

1. **Dyschoriste valeriana** Leonard, Field Mus. Nat. Hist., Bot. Ser. 18. 1937–38. TYPE: Costa Rica, *Standley & Valerio 46613* (US, not seen).—FIG. 9.

Herbs or suffrutescent *shrubs* to 50 cm high, erect or procumbent. *Stems* sometimes rooting at the basal nodes, quadrangular in the younger portions, strigose mostly at the angles. *Leaves* ovate to ovate elliptic, to 5 cm long and 2 cm wide, apically acute, basally attenuate, glabrous to sparingly puberulous along the costa above and beneath, the cystoliths numerous only above, cylindrical, ca. 1 mm long; petioles ca. 5 mm long, sparingly puberulous. *Inflorescences* in axillary clusters, the flowers subtended by elliptic leaflike bracts to 18 mm long and 6 mm wide, glabrous; bractlets oblanceolate to ca. 10 mm long, 2.5 mm wide. *Flowers* with the calyx lobes subulate to ca. 11 mm long and 1 mm wide at the base, ciliate; corolla blue or pale purple, funnelform, ca. 10 mm long,

FIGURE 9. *Dyschoriste valeriana* Leonard. Habit (×⅘). [After *Tyson* 6822 (MO).]

puberulous outside, glabrous inside, the tube 7 mm long, 2 mm wide at the base, 2.5 mm wide at the mouth, the limb slightly bilabiate, all the lobes oval, the 2 lobes of the lower lip divided to 2 mm long, 1.5 mm wide, 3 lobes of the upper lip to 3 mm long and 2 mm wide; stamens included, the longer filaments to 2 mm long, the shorter filaments 1 mm long, all glabrous, the anthers 1 mm long, minutely calcarate at the base of each cell; ovary glabrous. *Capsules* lanceolate, to 9 mm long, 1.75 mm broad, glabrous; seeds 2–4, obovate, flattened, ca. 1.5 mm long and 1 mm wide, densely mucilaginous puberulous when wet.

This species is found as a weed in open areas of Panama and Costa Rica at lower elevations.

PANAMÁ: El Llano, *Tyson* 6822 (MO).

10. ELYTRARIA

Elytraria Michx., Fl. Bor. Amer. 1: 8. 1803. nom. cons. TYPE: *E. virgata* Michx., nom. illeg. = *E. caroliniensis* (Gmelin) Pers.

Tubiflora Gmelin, Syst. Nat. 2: 27. 1791, nom. rejic. TYPE: *T. caroliniensis* Gmelin.

Herbs, caulescent or acaulescent. *Leaves* alternate or subopposite, basal or restricted to the terminal portion of the stem in a dense pattern, the cystoliths lacking. *Inflorescences* spicate, occasionally scapose, compact, the peduncles with imbricate, coriaceous bracts; bract single; bracteoles 2. *Flowers* perfect, zygomorphic, sessile, the calyx 4-merous, the segments narrow, entire or toothed apically; corolla 5-merous, white or blue, the tube narrow, 2-lipped with the upper lip 1-lobed, the lower lip 3-lobed; stamens 2, barely exserted, the anthers of 2 cells which are equal and parallel; ovary 2-celled, to 10 ovules in each cavity, the style 1. *Capsule* basally constricted and apically acute; seeds borne on papilliform funicles.

About 17 species have been described from southern North America and the New and Old World tropics.

1. **Elytraria imbricata** (Vahl) Pers., Syn. Pl. 1: 23. 1805.—FIG. 10.

Justicia imbricata Vahl, Ecolog. Amer. 1: 1. 1796. Collector and locality not given.

A weedy caulescent *herb*, occasionally acaulescent, to 40 cm high with a glabrous stem. *Leaves* mostly alternate and crowded at the upper portion of the stem, ovate lanceolate, 6–20 cm long, 1.5–6.0 cm wide, apically acute and basally attenuate, narrowing to a winged petiole, the upper surface pilose, the lower surface appressed pilose and restricted to the veins and the veinlets; margins undulate. *Inflorescences* on numerous scapes borne at the axils of the leaves, 5–28 cm long, branched or simple, covered with lightly appressed bracts; terminal spikes, one to several, 1.5–6.0 cm long; bract single, oblong to elliptic, 4–6 mm long, 1.5–2.0 mm wide, awn tipped and stiff with the upper bracts bearing 4 hyaline wings, 2 rounded wings extending from the base and 2 apical wings extending parallel to the apex; 2 subulate bractlets to 3 mm long with a ciliate costa. *Flowers* sessile; calyx 4-merous to 7 mm long, thin, transparent, with the lower segment bidentate; corolla pale lavender or blue, the tube 5–10 mm long. *Capsules* to ca. 3 mm long and 1 mm wide.

This species grows in shaded areas and in the open. It ranges from southwestern United States to Brasil along sandy areas of beaches at sea level, along roadsides and in slightly disturbed areas of cloud forest among trees.

CANAL ZONE: Forest along banks of Quebrada Fea, Quebrada Pura and canyon of Río Chagres, 70–100 m, *Dodge & Allen 17406* (MO). Between Summit and Gamboa, *Greenman & Greenman 5255* (MO). Madden Dam. *Lewis et al. 11* (MO). More or less forested slopes, *Macbride & Featherstone 2789* (MO). Farfan Beach area, *Tyson et al. 3179* (MO). Miraflores Lake, *White 265* (MO). CHIRIQUÍ: Palo Alto, E of Boquete, 5000 ft, *Stern et al. 1057* (MO). COLÓN: Juan Mina plantation, Río Chagres, 25 m, *Allen 4121* (MO). HERRERA: Road from La Avena to outskirts of Pesé, ca. 200 ft, *Burch et al. 1276* (MO). LOS SANTOS:

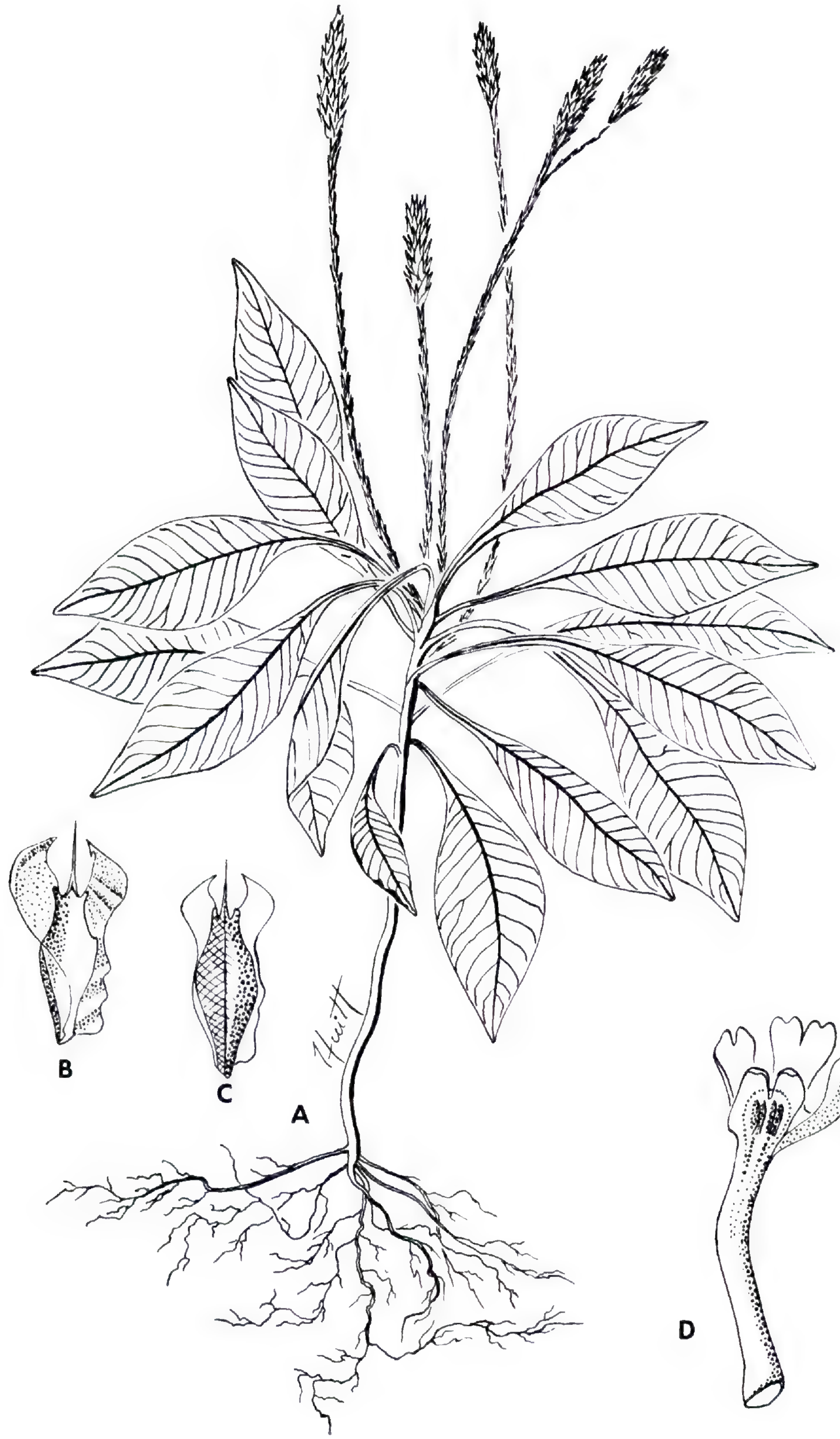

FIGURE 10. *Elytraria imbricata* (Vahl) Pers.—A. Habit (×⅗).—B. Bract (×10).—C. Seed (×16).—D. Corolla (×20). [After *Dodge & Allen 17406* (MO).]

Tonosí, *Stern et al. 1905* (MO). Monagre Beach, 5 mi SE of Chitré, *Tyson et al. 3055* (MO). PANAMÁ: Along trails, *Allen 103* (MO). Isla Taboga, 0–350 m, *Allen 1267* (MO).

11. GRAPTOPHYLLUM

Graptophyllum Nees, Wallich, Pl. Asiat. Rariores 3: 102. 1832. TYPE: *Justicia picta* L.

Shrubs. *Leaves* entire or dentate, often colored and variegated. *Flowers* pedicelled, in short, subsessile cymes, the panicles terminal or solitary in the axils of the leaves; calyx 5-merous; corollas reddish purple, bilabiate, the tube inflated above, the upper lip with 2 short, recurved lobes, the lower lip 3-lobed; stamens 2. *Capsules* clavate; seeds 2–4.

Ten species have been described for this genus. They occur in West Africa, New Guinea, Australia and Polynesia. None is native to the New World tropics.

1. **Graptophyllum pictum** (L.) Griff., Not. Pl. Asiat. 4: 139. 1854.—FIG. 11.

Justicia picta L., Sp. Pl., ed. 2. 21. 1762. TYPE: Herb Linn. (LINN 28.5, not seen, microfiche MO).

Graptophyllum hortense (L.) Nees in Wallich, Pl. Asiat. Rariores 3: 102. 1832. Based on *Justicia picta* L.

Shrubs to 3 m tall; stems glabrous. *Leaves* ovate to elliptic, to 20 cm long, 9 cm wide, apically acuminate, basally attenuate, glabrous, purplish or green, variously marked with yellow, the margins entire; petioles short. *Inflorescences* in terminal racemes, the rachis glabrous or sparingly puberulous; corollas dark purple or crimson, glabrous outside, glandular puberulous inside, to ca. 8 cm long, 1.5 cm broad at the mouth; stamens 2, exserted, staminodes 2. *Capsule* clavate; seeds 2–4.

This is a species which is cultivated in the gardens of tropical America. According to Bailey (1949) it is probably native to New Guinea.

PANAMÁ: Boca la Caja al lado de la iglesia, *Carrasquilla & Rincor 300* (MO).

12. HABRACANTHUS

Habracanthus Nees in DC., Prodr. 11: 312. 1847. TYPE: *H. silvaticus* Nees.

Herbs or *shrubs*. *Leaves* usually ovate to elliptic. *Inflorescences* in loose to dense panicles. *Flowers* with the calyx 5-merous, the segments narrowly lanceolate; corolla blue, red or yellow, salverform, bilabiate, the upper lip narrow, cuneate, the lower lip usually oblong cuneate, apically 3-lobed, the lobes rounded; stamens 2, exserted, divergent, the anthers 1-celled, the filaments attached below the middle of the anther; style exserted. *Capsules* clavate; seeds 4.

This is a genus of about 40 species found in Mexico, Central America and northern South America.

FIGURE 11. *Graptophyllum pictum* (L.) Griff. Habit (×1). [After *Carrasquilla & Rincor 300* (MO).]

1. **Habracanthus silvaticus** Nees in DC., Prodr. 11: 312. 1847. SYNTYPES: Mexico, *Linden 181* (K, not seen). Mexico, *Jurgensen 902* (K, not seen).—FIG. 12.

Shrub to 2 m tall; stems quadrangular when young, strigose along 2 lines. *Leaves* elliptic, to 13 cm long, ca. 5 cm wide, apically acuminate, basally acute, glabrous to sparingly puberulous along the costa and the veins, the cystoliths minute, relatively prominent on both surfaces, the margins undulate; petioles to 4 cm long, sparingly puberulous. *Inflorescences* in loose terminal thyrses to 11 cm long, 5 cm broad, the lateral branches of the thyrses dichotomously branched, the branches of the inflorescence sparingly strigillose; bracts subulate, to 6 mm long, 1 mm wide, puberulous; pedicels short, ca. 2 mm long, glabrous. *Flowers* with the calyx segments subulate, 5 mm long, 1 mm wide basally, glabrous; corolla blue, bilabiate, to ca. 3 cm long, glabrous, the tube 10 mm long, 1 mm broad, the lips to 20 mm long, the upper lip oblong, 2 mm wide, apically rounded, the lower lip elliptic, 5 mm wide, 3-lobed, the lobes 0.5 mm long, the middle lobe 1 mm wide, the lateral lobes 0.5 mm wide; stamens exserted to about the tip of the upper lip. *Capsules* (Leonard, 1938) 15 mm long, 2.5 mm in diameter; seeds flat, ca. 2 mm in diameter, puberulous and minutely roughened.

This species is found in wet forests and clearings of Mexico and Central America.

VERAGUAS: Santa Fé, forested slopes of Cerro Tute, 3000 ft, *Allen 4345* (MO, US).

13. HANSTEINIA

Hansteinia Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1854: 142. 1855. TYPE: *H. gracilis* Oerst.

Galeottia Nees in DC., Prodr. 11: 311. 1847, non Right Gal., 1845. TYPE: *G. gracilis* Nees, non *Hansteinia gracilis* Oerst.
Glockeria Nees in DC., Prodr. 11: 728. 1847, non Goeppert., 1836, new name for *Galeottia* Nees.

Herbs or *shrubs*; stems erect. *Leaves* elliptic or ovate; petiolate. *Inflorescences* in loose panicles which are sometimes thyrsoid. *Flowers* with the calyx segments 4 or 5, narrow, equal; corollas red, orange, yellow or white, cylindrical, basally narrow, abruptly expanded just above the calyx, somewhat obliquely enlarged and oblong, often constricted again at the mouth, the upper lip erect, the lower lip barely distinct from the corolla tube, 3-lobed; stamens 2, attached to the tip of the corolla tube, exserted, the anthers 1-celled, obtuse. *Capsules* clavate, glabrous, 4-seeded.

Fourteen species have been described for this genus, ranging from Mexico to Bolivia.

a. Leaves ovate to ovate elliptic, basally subcordate or rounded; stems and leaves pilose or subtomentose ..... 2. *H. ventricosa*
aa. Leaves elliptic or elliptic lanceolate (except for the uppermost pair which are ovate), basally attenuate (the uppermost pair, cordate or rounded); stems puberulous, the leaves mostly glabrous ..... 1. *H. reflexiflora*

FIGURE 12. *Habracanthus sylvaticus* Nees. Habit (×7/10). [After *Allen 4345* (MO).]

1. **Hansteinia reflexiflora** Leonard, Ann. Missouri Bot. Gard. 28: 465. 1941. TYPE: Panama, *Woodson & Schery 547* (MO, isotype).

Herbs, sometimes suffrutescent to 2 m tall, occasionally epiphytic; stems subterete in older portions, quadrangular in the younger portions, puberulous. *Leaves* elliptic or elliptic lanceolate, 3.5–11 cm long, 3 cm wide, apically acuminate, basally attenuate except for the uppermost pair which is subsessile, ovate,

and basally cordate or rounded, the cystoliths obscure, more visible beneath, glabrous except for strigillose hairs on the costa and the veins, the margins undulate; petioles to 5 mm long, puberulous. *Inflorescences* in terminal panicles to 25 cm long, 15 cm wide; bracts narrowly subulate, to 4 mm long, 0.5 mm wide, puberulous; peduncle, the rachis and the pedicels puberulous and with sparse glandular hairs to 1 mm long. *Flowers* generally reflexed, the pedicels 2–3 mm long; calyx 5-merous, the segments narrowly subulate, to 8 mm long, 0.5 mm wide basally, mostly glabrous, often reddish brown upon drying; corolla orange or red, to 2.8 cm long, glabrous, the tube slightly curved, 1.5 mm in diameter at the base, enlarged from the tip of the calyx to a tubular throat ca. 4 mm in diameter, the upper lip erect, oblong, 7 mm long, 3 mm wide, rounded except minutely bidentate and serrate apically, the lower lip short, truncate, 3-lobed, the lobes 1.5 mm long, 2 mm wide, apically acute; stamens exserted to ca. 6 mm beyond the upper lip, the filaments flat, glabrous; ovary glabrous. *Capsule* clavate, to 15 mm long, 3 mm broad, 2.5 mm thick, glabrous; seeds oval except for oblique base, flattened, 3 mm long, 2 mm wide, coarsely roughened.

This species is found in and adjacent to cloud forests of 1,000 to 2,000 m in Panama.

BOCAS DEL TORO: Róbalo Trail, northern slopes of Cerro Horqueta, 6000–7000 ft, *Allen 4940* (MO). CHIRIQUÍ: Disturbed cloud forest at Monte Rey above Boquete, *Croat 15794* (MO). Bajo Chorro, Boquete District, 6000 ft, *Davidson 91* (MO). NW of Boquete, Cerro Horqueta, 5000–5800 ft, *Dwyer et al. 456, 534* (both MO). Boquete Region, Cerro Horqueta, 6500 ft, *Hagen & Hagen 2027* (MO, US). Boquete, side of Sierra del Boquete, 1380 m, *Maurice 740* (US). Slopes approaching Cerro Horqueta, starting about 6.6 km NNE of Boquete, between 1500–1800 m, *Wilbur & Luteyn 19222* (DUKE). Bajo Mona and Quebrada Chiquero, 1500 m, *Woodson & Schery 547* (MO).

2. **Hansteinia ventricosa** (Donnell Smith) D. Gibson, Fieldiana, Bot., V. 34, no. 6, 63. 1972.—FIG. 13.

Glockeria ventricosa Donnell Smith, Bot. Gaz. 27: 439. 1899. TYPE: Costa Rica, *Pittier 3519* (CR).

Herb, sometimes suffrutescent, 3 m tall; stems terete in age, to subquadrangular when young, subtomentose, the hairs ca. 1 mm long. *Leaves* ovate to ovate elliptic, 7–15 cm long, 5–9 cm wide, apically acuminate, basally subcordate to rounded or obtuse, both the surfaces pilose, the hairs ca. 1 mm long, the cystoliths minute, the margins crenulate to undulate; petioles to 7 cm long, pilose. *Inflorescences* in terminal and axillary thyrses to 30 cm long, the rachises and the branches pilose; bracts oblong to narrowly lanceolate, to 7 mm long, 2 mm wide, acute to acuminate, pilose; pedicels to 2 cm long, flattened, puberulous and with occasional glandular hairs ca. 1 mm long. *Flowers* with the calyx 5-merous, the segments linear, to 7 mm long in flower and to 12 mm long in fruit, 1 mm wide, puberulous and with occasional glandular hairs; corolla orange, to 2.6 cm long, the tube curved outward, sparingly glandular pilose, 2 mm broad basally, contracting just above the ovary and then expanding abruptly to 5 mm just above the calyx lobes, the upper lip erect, elliptic, to 5 mm long, 2 mm wide, apically

FIGURE 13. *Hansteinia ventricosa* (Donnell Smith) Gibson. Habit (×½). [After *Allen 4937* (MO).]

bidentate, the lower lip ca. 1.5 mm long, 3-lobed, the lobes ca. 1 mm long, rounded; stamens exserted to ca. 1 cm beyond the tip of the upper lip. *Capsules* clavate, to 16 mm long, 3 mm wide, 3 mm thick, glabrous; seeds 4, oblong, basally oblique, 2 mm long, ca. 1.5 mm wide, flattened, coarsely roughened.

This species is found in forested areas above 1,000 m in Costa Rica and adjacent Panama. When observed under magnification of 10× or higher the hairs of stems, leaves and branches of the inflorescence are conspicuously banded a purplish color.

BOCAS DEL TORO: Róbalo Trail, northern slopes of Cerro Horqueta, 6000–7000 ft, *Allen 4937* (MO, US). Water Valley, Isla Colón, 0–120 m, *Wedel 784* (MO). CHIRIQUÍ: Cerro Punta, 2000 m, *Allen 1514* (MO, US). Bajo Chorro, Boquete District, 6000 ft, *Davidson 87* (F, MO). Valley of upper Río Chiriquí Viejo, 1300–1900 m, *White & White 11* (MO, US). Wooded slopes ca. 1 km N of Las Nubes, E of the mountain of Cerro Punta and ca. 5 km NW of the town of Cerro Punta, ca. 2000–2300 m, *Wilbur et al. 15221* (DUKE).

14. HEMIGRAPHIS

Hemigraphis Nees in DC., Prodr. 11: 722. 1847. TYPE: *H. latebrosa* (Roth) Nees.

Herbs; stems erect or ascending, rarely creeping. *Leaves* opposite, the margins undulate, crenate or entire. *Inflorescences* in terminal or axillary spikes, the flowers borne in the axils of conspicuous, imbricate bracts. *Flowers* with the calyx 5-merous, the segments subequal; corolla funnelform with a narrow tube, the tube straight or slightly curved, the limb spreading, the 5 lobes convolute in bud; stamens 4, didynamous, the filaments inserted at or below the mouth, the anthers 2-celled, blunt at the base, staminodes none; stigma bilobate, the lower lobe often inconspicuous. *Capsules* elliptic, seeds 6–12.

This is a genus of ca. 100 species in southern China, Indomalaysia and tropical Australia. One species is cultivated in gardens in Latin America and it occasionally escapes.

1. **Hemigraphis alternata** (Burm. f.) T. Anderson, J. Linn. Soc. Bot. 7: 114. 1864.—FIG. 14.

Ruellia alternata Burm. f., Fl. Indica 135. 1768. TYPE: Java, not seen.
Ruellia colorata Blume, Bijdr. 3: 795. 1826. TYPE: Java, not seen.
Hemigraphis colorata (Blume) Hallier, Nova Acta Leopoldiana, Abh. Deutsche Akad. Naturforscher 70: 199. 1897. [1898.]
Blechum cordatum Leonard, Carnegie Inst. Wash. Publ. 461: 200. 1936. TYPE: Belize, *Bartlett 11355* (MICH, not seen).

Herbs; stems ascending to 35 cm high, subquadrangular, sparingly puberulous, the roots emerging from the lower nodes. *Leaves* cordate, to 6 cm long and 4 cm wide, portions turning indigo upon drying, the apex obtuse, the base cordate, sparingly pilosulous on both surfaces, pilosulous at the costa, the cystoliths dense and prominent on the upper surface, to ca. 0.4 mm long, the margins crenate and sparingly ciliate; petioles to 2.5 cm long, pilose. *Inflorescences* axillary spikes on a peduncle to 1.5 cm long and 1 cm wide, the peduncle pilose; bracts ovate oblong, to 13 mm long and 4.5 mm wide, the apex acute, the base acute, puberulous on both the surfaces with dense, prominent cystoliths, turning indigo upon drying, the margins ciliate. *Flowers*, generally two per bract, the calyx segments slightly unequal, linear subulate, to 9 mm long, peeled, ciliate; corolla to 15 mm long, strigose at the throat adjacent to the stamens, minutely pubescent, the

FIGURE 14. *Hemigraphis alternata* (Burm. f.) T. Anderson. Habit (×9/10). [After *D'Arcy* 6675 (MO).]

ovary ciliate at the terminus, the style ciliate for the entire length. *Capsule* not seen.

This species is native to Malaysia and is cultivated in gardens in Latin America from which it occasionally escapes.

CANAL ZONE: Curundú, survival school area, *Tyson 1304* (MO). Weed in flower pot in front of Curundú Photo Service, *D'Arcy 6675* (MO).

15. HERPETACANTHUS

Herpetacanthus Nees in Moricand, Pl. Nouv. Amer. 159. 1847; Mart., Fl. Bras. 9: 93. 1847. TYPE: *H. longiflorus* Moricand.

Herbs or *shrubs*. *Inflorescences* spikes; bracts loosely imbricate. *Flowers* with the calyx 5-merous; corolla bilabiate; stamens 4, didynamous, the longer of each pair 2-celled with one of the cells superposed, the shorter of each pair 1-celled. *Capsules* clavate; seeds 4.

Ten species have been described in this genus. Most are from Brazil.

1. **Herpetacanthus panamensis** Leonard, J. Wash. Acad. Sci. 32: 185. 1942. TYPE: Panama, *Dunlap 554* (US, not seen).—FIG. 15.

Herbs, sometimes suffrutescent to 50 cm tall; stems ascending, sparingly branched, sometimes rooting at the lower nodes, young stem quadrangular, puberulous to pilose, the hairs reddish, old stem terete, glabrous. *Leaves* elliptic, to 13 cm long, 5.5 cm wide, apically acute to slightly acuminate, basally acute to attenuate, glabrous to pilose, and the cystoliths dense and prominent on both the surfaces, the margins undulate; petioles short, to ca. 3 mm long, puberulous to pilose. *Inflorescences* in terminal and axillary spicate panicles, the spikes to 3 cm long, 1 cm wide, the peduncles puberulous to pilose; bracts loosely imbricate, ovate to elliptic, to 13 mm long, 7 mm wide, apically acute, pilose, the margins ciliate; bracteoles alike, 2 mm wide. *Flowers* with 5-merous calyx to 4 mm long, the segments subulate, 3.5 mm long, 0.5 mm wide basally, glabrous outside, finely glandular puberulous inside, tipped by 1 or 2 hairs; corolla white, to 17 mm long, the tube 9 mm long, 1.5 mm wide basally, 3.5 mm wide at the mouth, the lips ca. 8 mm long, puberulous toward the tip, the upper lip ovate, 3.5 mm wide, apically minutely bidentate, the lower lip 3-lobed, the lobes 2 mm long, the middle lobe rounded, 2.5 mm wide, the lateral lobes acute, 1.5 mm wide, the longer of each pair of stamens barely exserted. *Capsules* clavate, sparingly puberulous, 10 mm long, 2.5 mm broad; seeds 4, flattened, ovate, 2.5 mm long, 2 mm wide, roughened.

This species is found in rain forests at lower elevations in Panama and Costa Rica. The hairs of stems, leaves and bracts have a purplish banding similar to that of *Hansteinia ventricosa*.

CANAL ZONE: Barro Colorado Island, Wheeler Trail, 1500, *Croat 11900* (MO); *Standley 40851* (US). COLÓN: Santa Rita lumber road, ca. 15 km E of Colón, forest, *Dressler & Lewis 3704* (MO).

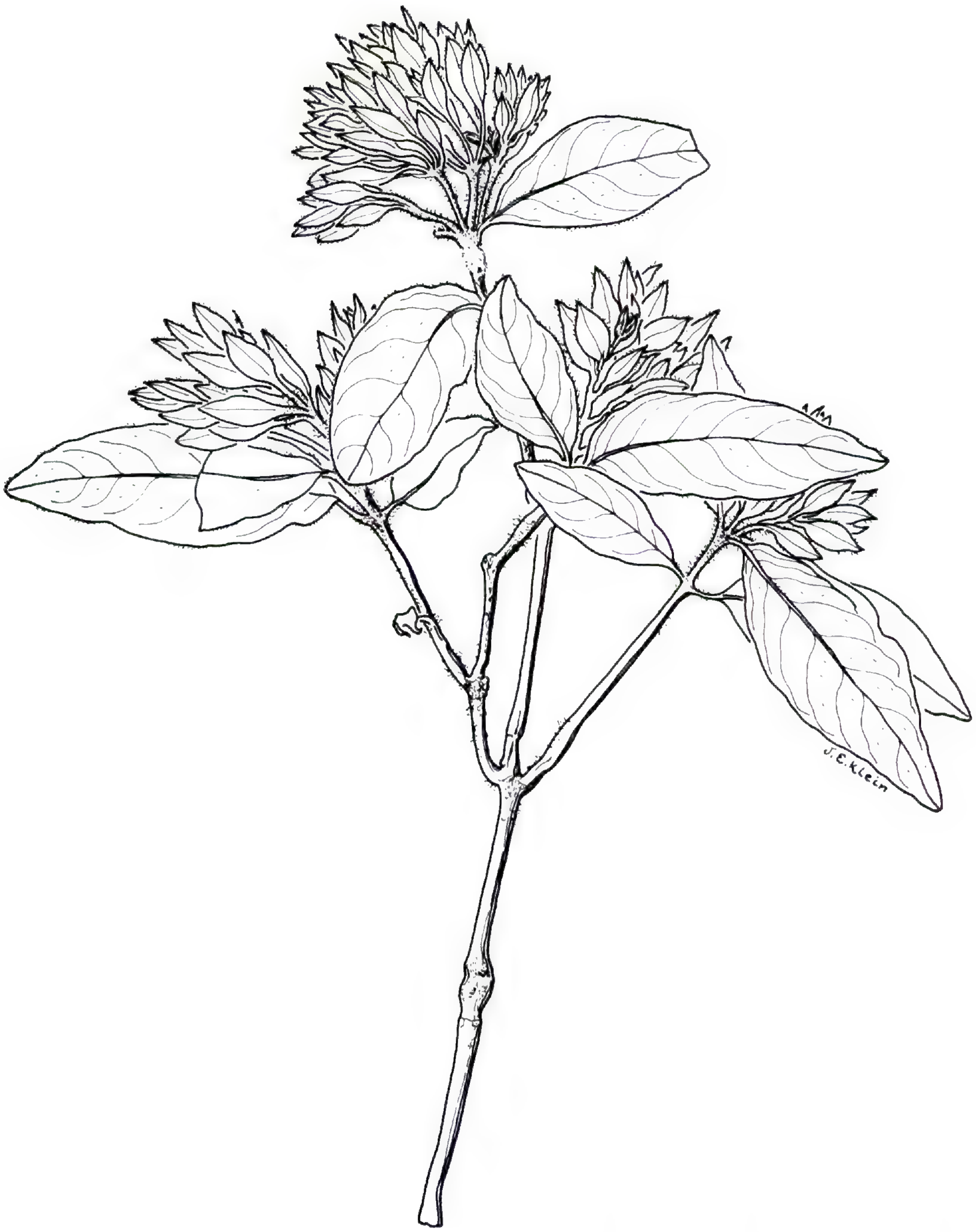

FIGURE 15. *Herpetacanthus panamensis* Leonard. Habit (×⅘). [After *Dressler & Lewis 3704* (MO).]

16. HYGROPHILA

Hygrophila R. Br., Prodr. 479. 1810. TYPE: *H. angustifolia* R. Br.

Herbs. Inflorescences in axillary fascicles; bracts linear. *Flowers* with the calyx 5-merous, the segments subequal; corolla tube cylindric, small, the limb 2-tipped; stamens 4 and didynamous, or 1 perfect stamen and a staminode in 2

pairs, the filaments of each pair united at the base, the anthers 2-celled, some mucronulate; posterior stigma lobe abortive; capsule oblong, nonstipitate; seeds 4–18 or more.

According to Leonard (1951) this genus is cosmopolitan. There are around 80 species.

1. **Hygrophila guianensis** Nees, London J. Bot. 4: 634. 1845. TYPE: British Guiana, *Schomburgk* 2nd collection, *331 (291)* (not seen).—FIG. 16.

H. conferta Nees in Mart., Fl. Bras. 9: 21. 1847. SYNTYPES: Brazil, *Pohl* (not seen) and Brazil, *Sellow* (not seen).

Herbs with branching, obtusely quadrangular stems to 1 m tall, glabrous. *Leaves* lanceolate, of various lengths on the same plant, from 2.5–25 cm long and 0.4–3 cm wide, the cystoliths generally numerous and prominent on the upper epidermis, less numerous beneath, the upper surface glabrous, the lower surface sparingly puberulous, mostly along the veins, apically and basally acuminate, entire to undulate. *Inflorescence* axillary, of clusters of 3 and 4, the flowers sessile. *Flowers* with the calyx 5-merous, the segments linear and equal, to ca. 8 mm long, white margined, puberulous; corolla white or yellowish white, the tube ca. 6.5 mm long, puberulous, 2-lipped, the upper lip 2-lobed, 3 mm long, the lower lip 3-lobed; stamens 4, didynamous, the filaments of each pair united at the base, the anthers 2-celled and parallel, the cells basally mucronulate. *Capsules* narrowly oblong, 9–13 mm long; seeds 6–8 per locule.

This species is found along streams and rivers or on the shores of ponds and lakes, often partly submerged and sometimes floating, from Mexico to Central Argentina.

BOCAS DEL TORO: Santa Catalina, *Blackwell et al. 2723* (MO). CANAL ZONE: Near Aguardiente Lagoon, Chagres River, *Chavez & Leguia s.n.* (DUKE). Barro Colorado Island, *Croat 6402* (MO). Chagres River, *Dwyer & Robyns 34* (MO); *Fairchild 2046, 2105* (both MO). Forest between Peluca Hydrographic Station and Quebrada Peluca along Río Boqueron, 70 m, *Steyermark & Allen 17228* (MO). COCLÉ: In stream above El Valle de Antón, *D'Arcy & D'Arcy 6726* (MO). Quebrada Amarillo, N of El Valle, *Witherspoon 8753* (MO).

17. JUSTICIA

Justicia[7] L., Sp. Pl. 15. 1753; Gen. Pl., ed. 5. 10. 1754. TYPE: *J. adhatoda* L.

Dianthera L., Sp. Pl. 27. 1753; Gen. Pl., ed. 5. 15. 1754. TYPE: *D. americana* L.
Adhatoda Medic., Act., Acad. Theod. Palat. 6. Phys. 393. 1790; TYPE: *Justicia adhatoda* L., fide Leonard.
Leptostachya Nees in Wallich, Pl. As. Rar. 3: 76, 105. 1832. SYNTYPES: *L. virgata* Nees and *L. wallichii* Nees.
Belaperone Nees in Wallich, Pl. As. Rar. 3: 76, 102. 1832. TYPE: *B. amherstiae* Nees.
Rhytiglossa Nees in Lindl., Introd. Nat. Syst. ed. 2. 444. 1836. SYNTYPES: *R. origanoides* Nees, *R. eckloniana* Nees, and *R. cilata* Nees.
Jacobinia Nees ex Moric., Pl. Nouv. Am. 156, *tab.* 92. 1846. TYPE: *J. lepida* Nees ex Moric. type cons.

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[7] More generic synonyms are provided by Leonard (1958). Only names relating to Panamanian material are listed here.

FIGURE 16. *Hygrophila guianensis* Nees.—A. Habit (×½).—B. Capsule (×½). [After *D'Arcy & D'Arcy 6726* (MO).]

Herbs or *shrubs*. *Leaves* petiolate, usually ovate to elliptic and entire. *Inflorescences* usually of spikes or panicles, occasionally in cymes or solitary; bracts various, small and distant, linear or subulate to large, conspicuous and imbricate. *Flowers* with the calyx segments usually narrow and equal, some unequal, mostly 5(4)-merous; corollas bilabiate, the corollas usually white, pink or purple, the tube usually narrow, funnelform, the upper lip 2-lobed, the lower lip 3-lobed; stamens 2, usually slightly exserted but not exceeding the corolla lip, the anther cells 2, usually unequal, often superposed, with one or both cells apiculate or calcarate, the connective narrow to broad. *Capsules* clavate, 4-seeded.

This genus may be recognized by its 2 slightly exserted stamens with anthers having 2 cells which are frequently unequal, superposed and apiculate or calcarate basally. This plus the bilabiate, narrow-tubed corollas and the lack of staminodes are useful features.

This is a large, cosmopolitan genus of approximately 420 species found in both the tropical and temperate climates of the New and Old World.

a. Inflorescences in panicles or thyrses (cymose panicles).
  b. Leaves large, to 40 cm long; inflorescence a dense thyrse ..... 3. *J. aurea*
  bb. Leaves under 30 cm long; inflorescences paniculate or loose thyrses.
    c. Rachis of inflorescence pilose, or hairs retrorsely curved; corollas curved outward ..... 15. *J. secunda*
    cc. Rachis of inflorescence glabrous or inconspicuously puberulous or glandular puberulous; corollas mostly straight.
      d. Calyx segments 4; leaves metallic blue beneath ..... 10. *J. metallica*
      dd. Calyx segments 5; leaves colored otherwise.
        e. Plant a long vine; calyx segments over 1.5 cm long ..... 8. *J. graciliflora*
        ee. Plants an erect herb or shrub; calyx segments under 1.5 cm long.
          f. Leaves crenate; bracts to 7 mm long ..... 7. *J. crenata*
          ff. Leaves entire, undulate or crenulate; bracts to 3 mm long.
            g. Leaves apically and basally obtuse or rounded; stems rooting at the lower nodes ..... 5. *J. chamaephyton*
            gg. Leaves apically acuminate, basally variable but mostly acute or attenuate; stems not rooting at the nodes.
              h. Corollas under 2 cm long; leaves mostly lanceolate (excepting *J. pectoralis* var. *macrophyllus*).
                i. Corollas 7–12 mm long; inflorescence all terminal.
                  j. Leaves lanceolate; branches of inflorescences with glandular hairs ..... 13a. *J. pectoralis* var. *pectoralis*
                  jj. Leaves oblanceolate or elliptic; branches of inflorescence without glandular hairs ..... 13b. *J. pectoralis* var. *macrophyllus*
                ii. Corollas under 7 mm long; inflorescences both terminal and axillary ..... 6. *J. comata*
              hh. Corollas over 2 cm long; leaves elliptic or ovate.
                k. Calyx segments unequal; branches of inflorescence glandular-puberulous ..... 11. *J. oerstedii*
                kk. Calyx segments equal; branches of inflorescence glabrous ..... 16. *J. tinctoria*

aa. Inflorescences in spikes or cymes.
  l. Inflorescences in axillary cymes; bracts 3 mm long or less.
    m. Leaves of a pair unequal; corolla violet or pale purple ..... 17. *J. trichotoma*

mm. Leaves of a pair equal; corolla orange red to yellowish ..... 9. *J. macrantha*
ll. Inflorescences in spikes borne singly or in clusters; bracts 6–18 mm long.
n. Bracts over 13 mm long.
o. Corolla over 25 mm long; leaf bases obtuse to rounded .. 4. *J. carthaginensis*
oo. Corolla under 25 mm long; leaf bases attenuate. ..... 1. *J. adhatoda*
nn. Bracts under 13 mm long.
p. Leaves to 6.5 mm long, basally obtuse to rounded; anther cells strongly superposed by a connective 3.5 mm wide ..... 12. *J. panamense*
pp. Leaves over 12 cm long, basally attenuate or acute; anther cells closer together, the connective not over 1 mm wide.
q. Corolla under 1.5 cm long; bracts ciliate ..... 14 .*J. refractifolia*
qq. Corolla over 3 cm long; bracts not ciliate.
r. Corollas white; calyx puberulous ..... 18. *J. urophylla*
rr. Corolla bright pink; calyx glandular puberulous ..... 2. *J. allenii*

1. **Justicia adhatoda** L., Sp. Pl. 15. 1753. TYPE: Ceylon, from cultivation (not seen).

Shrub to 1.25 m tall; stems subquadrangular, with dense golden yellow, strigose or pilose hairs in the young portions. *Leaves* elliptic, 7–17 cm long, 2.5–8 cm wide, apically acuminate with rounded tips, basally attenuate, sparingly strigose to strigose above, strigose beneath, more dense at the costa above and beneath making the costa appear golden yellow, drying dark green above sometimes with a reddish brown cast, light green beneath; petioles 0.5 to 2.5 cm long, pubescence as on the stem. *Inflorescences* in compact terminal and axillary spikes to 6 cm long and 2 cm wide; bracts obovate to ovate, often asymmetrical, to 1.7 cm long and 1 cm wide, apically obtuse to acute, glandular puberulous on both surfaces, drying mostly to a dark reddish brown, ciliate; bracteoles elliptic oblong, to 12 mm long and 3 mm wide; rachis densely pilose glandular; peduncle 5–15 mm long, pubescence as on the stem. *Flowers* sessile, calyx 5-merous, equal, the lobes linear lanceolate, to 11 mm long and 1 mm wide at the base, glandular puberulous; corolla white to pink or purplish, ca. 20 mm long, bilabiate, the tube 13 mm long, 2 mm wide at the base, 2.5 mm wide at the throat, the upper lip erect, 15 mm long, 2.5 mm wide at the base, apically notched, the lower lip 3-lobed, each lobe elliptic, ca. 6.5 mm long, 2.5 mm wide, apically obtuse, the upper corolla puberulous outside, glabrous inside, lower half glabrous; stamens exserted ca. 5 mm beyond the mouth of the corolla, the filaments ca. 5 mm long, glabrous, the anther cells 1 mm long, unequal, the upper cell 1 mm above the lower cell, the lower cell apiculate. *Capsule* puberulous; seeds orbicular, 2–2.5 mm wide, glabrous.

This species is found in or along forested areas in only one locality in Panama.

PANAMÁ: Cerro Jefe along main road before turnoff to summit, *Croat 13054* (MO). Cerro Jefe, 2900 ft, *Dwyer & Gentry 8489* (MO). Near top of Cerro Jefe to 1 mi beyond, *Dwyer et al. 3440* (MO). La Eneida, Cerro Jefe region, 750 m, *Maas & Dressler 677* (MO). Gorgas Memorial Labs yellow fever research camp, "Campamiento Quatro," 5–10 km NE of Altos de Pacora, 600 m, *Mori & Kallunki 3424* (MO). Road from Cerro Azul to Cerro Jefe, 2300–2700 ft, *Tyson 5306* (MO). Slopes of Cerro Jefe between Cerro Azul and La Eneida ca. 15 mi NE of Panama City, *Wilbur et al. 15541B* (DUKE).

2. **Justicia allenii** (Leonard) Durkee.[8]

Belaperone allenii Leonard, Proc. Biol. Soc. Wash. 56: 55. 1943. TYPE: Panama, *Allen* 2285 (US, holotype; MO, isotype).

Shrub or suffrutescent herb to 1.5 m tall; stem quadrangular in younger portions, glabrous. *Leaves* ovate elliptic, to 15 cm long and 6.5 cm wide, apically acuminate, basally attenuate, glabrous, the costa and the veins, 12–16 pairs, prominent, the cystoliths dense though minute, visible on both the surfaces, the margins entire to undulate; petioles 1–3 cm long, glabrous. *Inflorescences* of 2–3 terminal or axillary spikes, each 2–3 cm long, the primary peduncle ca. 5 cm long, glabrous, the secondary peduncles ca. 1.25 cm long, puberulous; bracts at apex of primary peduncle linear, 6–12 mm long, ca. 1 mm wide, glabrous, apically obtuse, bracts subtending the flowers subulate, 5–6 mm long, 1.5 mm at base, puberulous; bracteoles similar to the bracts, though a little smaller. *Flowers* with a deeply lobed, 5-merous calyx, the lobes linear lanceolate, 10–11 mm long, 1.5 mm wide, apically acuminate, glandular puberulous; corolla bright pink, bilabiate, to 5.5 cm long, narrowly funnelform, 2 mm wide at base, 6 mm wide at the mouth, glandular puberulous outside, glabrous inside, the lips about equal, to 2 cm long, the upper lip 2-lobed, the lobes 1 mm long, obtuse, the lower lip 3-lobed, the lobes rounded, the middle lobe to 3.5 mm wide, the lateral lobes 3 mm wide; stamens exserted to about the notch of the upper lip, the anther cells approximate, superposed, the upper cell basally apiculate, the lower cell with a blunt basal spur ca. 1 mm long; ovary glabrous, the style 4 cm long, puberulous, the stigma 2-lobed, the lobes minute, conical. *Fruit* not seen.

According to Leonard this species is not closely related to other Central American species of the genus. The collector states that the species is a fairly common undershrub along trails in the area where it was collected.

COCLÉ: Hills N of El Valle, 800–1000 m, *Allen* 2285 (US). Cerro Pajita, hills N of El Valle, 1100 m, *Allen* 3788 (MO). Trail to Cerro Pajito, N of El Valle, 800 m, *Allen* 3932 (MO).

3. **Justicia aurea** Schlecht., Linnaea 7: 393. 1832, non *Jacobinia aurea* Hiern. (1877). TYPE: Mexico, *Schlechtendal* (B.?; not seen).

J. umbrosa Benth., Pl. Hartw. 79. 1841. TYPE: Mexico, *Hartweg* 552, (not seen). fide Leonard.
Jacobinia aurea (Schlecht.) Hemsl., Diag. Pl. Nov. 2: 35. 1879.
Jacobinia umbrosa (Benth.) Blake, Contr. Gray Herb. 52: 103. 1917.

Shrub to 3.5 m tall; stem subquadrangular when young, tomentose. *Leaves* ovate to ovate elliptic, 15–40 cm long, 8–17 cm wide, apically acuminate, basally attenuate, glabrous to sparingly strigose above, the hairs more dense on the costa, glabrous to strigose beneath, hairs more dense at the costa, the cystoliths dense and prominent on the upper surface, the margins entire, undulate or crenulate; petioles 1–9 cm long, tomentose. *Inflorescences* densely thyrsoid at or near the ends of the branches, 8–33 cm long, ca. 5 cm wide excluding the flowers, the

[8] *Justicia allenii* (Leonard) Durkee, comb. nov.

rachises tomentose; bracts linear lanceolate, mostly 11 mm long, 1–2 mm wide, the bracteoles similar though a little smaller, both puberulous. *Flowers* with 5-merous calyx, the segments lanceolate, to 7 mm long, 1.5 mm wide at the base, puberulous; corolla yellow, bilabiate, cylindrical, to 5.5 cm long, 3 mm wide, puberulous-glandular outside, glabrous inside except for bearded throat, the lips ca. 2.5 cm long, the upper lip erect, 7 mm wide, apically acute, the lower lip 6 mm wide, apically 3-lobed, the lobes ca. 1 mm long, apically rounded and slightly hooded, especially the middle lobe; stamens exserted to about the tip of the upper lip, the anthers 3 mm long, glabrous, the cells unequal, basally acute, the filaments stout, ca. 0.75 mm wide, glabrous; ovary 2 mm long, 1 mm wide, glabrous. *Capsule* puberulous, clavate, 2.0–2.5 cm long, ca. 5 mm wide, 4 mm thick; seeds 4, flattened, suborbicular, ca. 2 mm in diameter, the surface roughened.

This species is found in moist habitats along stream banks, trails, roads and clearings to about 2,000 m in southern Mexico and Central America.

CHIRIQUÍ: "New Switzerland," central valley of Río Chiriquí Viejo, 1800–2000 m, *Allen 1418* (MO). NW side of Cerro Pando, *Croat 15946* (MO). Roadside between Cerro Punta and Bajo Grande, *Croat & Porter 16013* (MO). Top of peak between Baru and Respinga, 3000 m, *D'Arcy 10128* (MO). Bajo Mono, Boquete District, *Davidson 563* (MO). NW of Boquete, Cerro Horqueta, 5000–5800 ft, *Dwyer et al. 521* (MO). Slopes of Cerro Punta, ca. 2000 m, *Gentry 5862* (DUKE, MO). Valley of upper Río Chiriquí Viejo, *P. White 338* (MO). Río Chiriquí Viejo Valley, *P. White 1577* (MO). NW side of mountain of Cerro Punta beyond Las Nubes, ca. 7500 ft, *Wilbur & Teeri 13216* (DUKE). Weedy trail and cut-over slopes ca. 2 km W of La Garita, ca. 3 km WNW of Cerro Punta at 2000 m, *Wilbur et al. 15274* (DUKE). COCLÉ: Region N of El Valle de Antón, 800–1000 m, *Allen 2927, 3695, 3713* (all MO). El Valle, on edge of bog, ca. 2700 m, *Dwyer 162* (MO). El Valle, village, *Dwyer 1842* (MO). DARIÉN: Path from Pucro to Río Pucro, *Duke 5362* (MO). El Real airport, 1 mi from Panamerican Highway, *Sexton 254* (MO). SAN BLAS: Mountains above Puerto Obaldía, *Gentry 1500* (MO). VERAGUAS: 5 mi W of Santa Fé on road past Escuela Agrícola de Alto Piedra on Pacific side of divide, 800–1200 m, *Liesner 852a, 845* (both MO). NW of Santa Fé, 2 km from Escuela Agrícola Alto de Piedra, *Mori & Kallunki 5224* (MO).

4. **Justicia carthaginensis** Jacq., Enum. Pl. Carib. 11. 1760. TYPE: Caribbean *Rohr* (not seen).

Adhatoda carthaginensis (Jacq.) Nees, in DC., Prodr. 11: 403. 1847.

Herbs, sometimes suffrutescent, to 1.25 m high; stems erect, tetrangular and sulcate, sparingly pilose in grooves when young, glabrous in age. *Leaves* ovate to ovate lanceolate, to 4.8 cm wide and 9 cm long, apically acuminate, basally obtuse to rounded, decurrent on the petiole, glabrous to strigose mainly on the veins on both the surfaces, the veins 7–8 pairs, moderately prominent on both the surfaces, the margins entire, ciliate; petioles to 2 cm long, hirtellous. *Inflorescences* mostly in compact terminal spikes, sometimes both terminal and axillary, to 9 cm long, 2 cm wide; one oblanceolate-spatulate bract subtending each flower, 1.2–1.8 cm long, 0.3–1.1 cm wide, apiculate, glabrous inside, outside with glandular hairs mostly toward the apex, glandular puberulous toward the middle, ciliate; 2 bracteoles subtending each flower, oblanceolate spatulate, to 11 mm long, 1.8 mm wide, glabrous inside, outside with glandular hairs toward the apex, glandular puberulous toward the middle, the margins ciliate; pubescence of rachis similar to that of the stem. *Flowers* sessile, the calyx 5-merous, equal, the lobes narrowly

lanceolate, ca. 8 mm long, puberulous, the margins white and ciliate; corolla reddish violet, violet, or purple, the lips to 2 cm long, the upper lip erect, notched, the lower lip 3-lobed, the lobes obtuse, the middle lobe 7.5 mm wide, the lateral lobes 5.5 mm wide, glandular-puberulous outside, glabrous inside, the tube 10 mm long, 3 mm wide at the base, 5 mm at the throat, the middle lobe of lower lip personate, the tube bearded at 4 points just above the ovary; stamens exserted ca. 10 mm beyond the mouth of the corolla tube, the filaments 11 mm long, glabrous, the anther cells 2 mm long, unequal, the upper cell 1 mm above the lower cell, the lower cell spurred, the upper cell blunt; style ca. 20 mm long, puberulous toward the base, the stigma 2-lobed. *Capsules* clavate, to 15 mm long, 6 mm broad and 3 mm thick, puberulous, the retinaculum stout, 3 mm wide and 1 mm thick; seeds 4, nearly spherical, 3 mm across, 1.7 mm thick, puberulous, light to dark brown at maturity.

This species is found on roadsides and waste places, often in coastal areas, more commonly at lower elevations.

BOCAS DEL TORO: Isla Colón, SW of Bocas at Maccaw Hill, 0–120 m, *Wedel 564* (MO). Old Bank Island, Chiriquí Lagoon, *Wedel 2078A* (MO). Isla Colón, Chiriquí Lagoon, *Wedel 2837, 2951* (both MO). CANAL ZONE: Near Boy Scout Camp, *Croat 12915* (MO). Along old Gamboa road between Summit Hills Golf Course and Summit Naval Radio Station, *Croat 16662* (MO). In Government forest along Las Cruces Trail, 75 m, *Hunter & Allen 670* (MO). COCLÉ: Banks of Rio Grande, *Burch et al. 1179* (MO). 10 mi E of Nata at Rio Grande, *Tyson 5270, 5276* (both MO). HERRERA: Chitré, ca. 20 m, *Allen 1099* (MO). PANAMÁ: Taboga Island, 300 m, *Allen 141, 1294* (both MO). Canitas de Chepo, a orillas del Rio Rumagati, *Carrasquilla et al. 271* (DUKE). Taboga Island, *Durkee et al. 71–163* (MO). Riomar, Playa near Río Mar, open pastureland, *Ebinger 511* (MO). Majé, old forest, fairly flat, ca. 5 mi up the Río Nuevo, *Foster & Kennedy 1988* (DUKE). Río Pasiga to above waterfall on second main fork, *Gentry 2305* (MO). Near stream, Icanti, Río Agua Clara, *Gentry 2600* (MO). Local, *Porter et al. 5174* (MO). W of Chepo on road to Panama City, *Tyson 5365* (MO). El Llano, *Tyson 6819* (MO). Weedy roadsides within 1 mi of Chepo, *Wilbur & Luteyn 11824* (DUKE). Local, *Woodson et al. 1472* (MO).

5. **Justicia chamaephyton** D. Gibson, Fieldiana, Bot. 34(6): 67. 1972. Based on *Belaperone variegata* Lindau.

B. variegata Lindau in Pittier, Primit. Fl. Costaric. 2: 315. 1900, non *Justicia variegata* Aubl. (1775) fide Gibson. TYPE: Costa Rica, *Tonduz 6735* (B.?; not seen).

Suffrutescent *herb* to 0.5 m tall; stems ascending, rooting at lower nodes, terete to subquadrangular near the apex, the brown puberulous hairs retrorse. *Leaves* elliptic, 6–11 cm long, 3.5–6 cm wide, apically and basally obtuse or rounded, glabrous above, the veins and the costa puberulous beneath, the cystoliths dense and conspicuous on both the surfaces, the margins entire to crenulate; petioles short, 3–5 mm long, puberulous. *Inflorescences* in terminal, spicate panicles, the spikes to 12 cm long, the peduncles and the rachises puberulous, the internodes 10–15 mm long at the base of spike; bracts subulate, ca. 3 mm long, basally 1 mm wide, puberulous; bracteoles similar, but smaller. *Flowers* with 5-merous calyx, the segments slightly unequal, all linear subulate, posterior and lateral segments 6 mm long, ca. 1 mm wide basally, posterior segment 4 mm long, all the segments puberulous; corolla light purple, to 13 mm long, puberulous, the tube 1.5 mm wide at base, 2 mm wide at mouth, the lips to 7 mm long, the

upper lip 3 mm wide at the base, apically minutely bilobed; lower lip 4.5 mm wide, 3-lobed, the lobes 2 mm long, the middle lobe 2 mm wide, the lateral lobes 1.5 mm wide, all apically rounded; anther cells superposed, the lower cell spurred, the filaments with minute glandular hairs on exserted portion. *Capsules* clavate, ca. 10 mm long, 3 mm wide, puberulous; seeds light brown, orbicular, flattened, 2.5 mm in diameter, glabrous.

This species is found in or adjacent to rain forest at low elevations in Costa Rica and Panama.

BOCAS DEL TORO: Forest above RR stop at Milla 7.5, *Croat & Porter 16290* (MO). Quebrada Huron, rapid streams through evergreen seasonal forest, *Kirkbride & Duke 427* (MO). Water Valley, *Wedel 603, 916* (both MO, US); *Wedel 917* (US). CHIRIQUÍ: David airport, 25 ft, disturbed grassland and edge of marsh, *Lewis et al. 851* (MO). DARIÉN: Cativo Swamp, Río Chucunaque, ca. ½ hour below Mortí, *Duke 11747* (MO). Río Chucunaque, camp Ortiga in freshwater swamp forest, 131 ft, *Duke 15524* (MO). SAN BLAS: Forests around Puerto Obaldía, 0–50 m, *Pittier 4281* (US).

6. **Justicia comata** (L.) Lam., Encycl. Méth. 1: 632. 1783.

Dianthera comata L., Syst. Nat., ed. 10, 850. 1759. TYPE: Jamaica, *Sloane* (not seen).

Suffrutescent *herbs*, mostly 0.5–1.0 m tall; stems erect to ascending, often rooting at the lower nodes, mostly branched, the younger stems somewhat grooved and hexagonal, glabrous to pilose. *Leaves* somewhat variable, lanceolate, ovate, elliptic or elliptic oblong, to 12 cm long, 3.5 cm wide, apically acuminate, basally acute, rounded or obtuse, glabrous to sparingly strigose along the costa, the cystoliths dense on both the surfaces, especially on the upper surface, the margins entire to slightly undulate; petioles to 1 cm long, glabrous to strigose, sometimes obsolete. *Inflorescences* in terminal and axillary spicate panicles, the spikes whorled at the rachis nodes, the flowers secund on the peduncle, the rachis and the branches grooved with the branches generally somewhat flattened also; rachis and branches puberulous, sometimes with a few longer glandular hairs; bracts subulate, ca. 2 mm long, 0.5 mm wide, keeled; bracteoles similar, slightly shorter. *Flowers* sessile with 5-merous calyx, segments equal, lanceolate, to 3 mm long, 0.4 mm wide at the base, glabrous; corolla bilabiate, white, purplish, light green, or white with purplish dots or streaks, 4–6 mm long, 0.8 mm wide at the base, inflated to 1.5 mm just above the base, glabrous; tube 3 mm long, the upper lip 3 mm long, 1.8 mm wide at the base, the apex acute, the lower lip 4 mm long, 1.5 mm wide at the base, expanding to 3 mm wide above, 3-lobed at the tip, the lobes about equal, 0.5 mm long, 1 mm wide, obtuse at the apex; stamens exserted ca. 2 mm beyond the corolla mouth, the filaments pilose at the base, glabrous above. *Capsules* clavate, 4–5 mm long, 2 mm broad, 1 mm thick; seeds 4, reddish brown, suborbicular, ca. 1 mm, flattened, ca. 1 mm in diameter, papillose.

Growing in waste places throughout tropical America, this species is generally found at 500 m or lower. It is found in both damp and dry locations. Because this plant is found over such a wide range it displays considerable variation.

BOCAS DEL TORO: Santa Catalina, *Blackwell et al. 2727a* (MO). RR near station at Milla 10, *Croat & Porter 16336* (MO). Hillside above Almirante, *Gentry 2705* (MO). 10–15 mi

inland S from mouth of Río Changuinola, *Lewis et al. 891A, 985* (both MO). Chiriquicito to 5 mi S along Río Guarumo, *Lewis et al. 1958, 1959, 2043* (all MO). Isla Colon, *Wedel 77* (MO). Water Valley, Isla Colon, 0–120 m, *Wedel 612* (MO). Chiriquí Lagoon, *Wedel 432, 934, 1455, 2071, 2593, 2629* (all MO). CANAL ZONE: Fort San Lorenzo, *Burch et al. 1037* (MO). Pipeline Road at Río Agua Salud, on creek bank, *Croat 12343* (MO). Open lowland just E of Gatun Locks, *Duke 4308* (MO). Near Beach at Ft. Kobbe, low wooded inland area, *Duke 4707* (MO). K-9, at bridge, *Dwyer 3011* (MO). Albrook, *Dwyer 7117* (MO). Río Chagres, *Fairchild 2106* (MO). Coco Solo, *Gentry 6472* (MO). Barro Colorado Island, *Lewis et al. 5212* (MO). Gaillard Highway just N of Paraiso, *Lewis et al. 5368* (MO). Summit Gardens, 0–100 m, *Mori & Kallunki 1780* (MO). Ft. Clayton, Cardenas Creek area, *Tyson 1286* (MO). Gamboa, *Tyson et al. 4582* (MO). Ft. Gulich, collector unknown (MO). CHIRIQUÍ: Burica Peninsula, Rabo de Puerco, 10.5 km W of Puerto Armuelles, 100 m, *Busey 521* (MO). Boquete, Cerro Horqueta, 5000–6000 ft, *Dwyer & Hayden 7719* (MO). San Bartolome, Peninsula de Burica, 0–50 m, *Woodson & Schery 874* (MO). COLÓN: Miguel de la Borda, swampy area, *Croat 9839* (MO). Road to Portobelo between Río Piedras and Portobelo, *Elias & Kirkbride 1651* (MO). Ca. 0.5 km from the Río Buenaventura near Portobelo, *Kennedy & Gra 2245* (MO). DARIÉN: El Real around town, *Burch et al. 1065* (MO). Ascent of Cerro Pirre from Río Pirre S of El Real, 750–1030 m, *Duke 5357* (MO). Río Sambú, 0.5 mi above Río Venado, *Duke 9295, 9311* (both MO). Forest 1–4 mi N of Pucro, *Duke 13021* (MO). Quebrada Camachimuricate cerca casa de Bartolo, *Kennedy 2845* (MO). Camp Summit, Darién-San Blas border along Sea Level Canal Rt. 17, 1000–1200 ft, *Oliver et al. 3672* (MO). Streamside, woods 2 mi E of Santa Fé, *Tyson et al. 4809* (MO). Peak ca. 300 ft high between Ríos Balsa and Areti at their confluence, *Duke 8729* (MO). PANAMÁ: El Llano, *Duke 5502* (MO). Majé, ca. 5 mi up the Río Nuevo, a major branch of the Río Majé, *Foster & Kennedy 1987* (DUKE). El Llano, marsh near Bayano, *Gentry & Tyson 1715* (MO). Icanti, Río Agua Clara, *Gentry 2622* (MO). Falls of La Chorrera, along stream, wet forest, *Lewis et al. 5212* (MO). El Llano, *Tyson 6820* (MO). SAN BLAS: Above Ailigandi River, *Duke & Bristan 344* (MO). Headwaters of Río Cuadi, Camp Diablo, Drill Site 22, N 82.2, E 87.8, seasonal evergreen forest along river, 273.4 ft, *Duke et al. 3628* (MO).

7. **Justicia crenata** (Leonard) Durkee.[9]

Jacobinia crenata Leonard, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1938. TYPE: Costa Rica, *Donnell Smith 6691* (US, not seen).

Shrub to 5 m tall; stems terete, glabrous. *Leaves* elliptic, to 24 cm long, 9.5 cm wide, apically acuminate, basally attenuate, glabrous, numerous cystoliths clearly visible on both surfaces, the margins crenate; petioles to 5 cm long, glabrous. *Inflorescences* in terminal, loosely spicate panicles, the spikes to 6 cm long, the internodes of the spikes ca. 5 mm long, the peduncles and the rachises puberulous; bracts elliptic, to 7 mm long, 2 mm wide, sparingly glandular puberulous, apically rounded to acute, soon deciduous; bracteoles similar but smaller. *Flowers* with 5-merous calyx, the segments linear lanceolate, to 7 mm long, 1.25 mm wide at base, sparingly glandular puberulous, the margins minutely ciliolate; corollas red with yellow tip, to 5 cm long, bilabiate, puberulous glandular, the tube narrow, 3 mm wide at the base narrowing to 2 mm wide above the ovary, 6 mm wide at the mouth, the lips erect, each to 2.5 cm long, 6 mm wide, gradually narrowing from the base to tip, the upper lip apically notched, the lower lip with 3 small lobes at the apex, the lobes each ca. 2 mm long, rounded and hooded at the tip; stamens exserted to the tip of the lobes, the anther cells unequal, each to 2.5 mm long, each basally slightly spurred, the lower cell more so. *Capsules* (Leonard, 1938) clavate, 1.5 cm long, glabrous or with a few glandular hairs at the tip.

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[9] *Justicia crenata* (Leonard) Durkee, comb. nov.

This species is found in rain forests of Costa Rica and adjacent Panama.

BOCAS DEL TORO: Chiriquicito to 5 mi S along Río Guarumo, rain forest by river, *Lewis et al. 2118* (MO). Water Valley, *Wedel 747, 1436* (both US). Chiriquí Lagoon, Fish Creek, *Wedel 2183* (MO).

8. **Justicia graciliflora** (Standley) D. Gibson, Fieldiana, Bot. 34: 69. 1972.

Belaperone graciliflora Standley, Contr. Arnold Arbor. 5: 142. *tab. 20.* 1933. TYPE: Panama, *Shattuck 602* (MO, US).

Suffrutescent *vine* climbing to 10 m; stems terete, glabrous to strigulose in 2 lines. *Leaves* elliptic, to 11.5 cm long, 4.5 cm wide, apically acuminate to obtuse, basally attenuate, glabrous, the cystoliths prominent on both the surfaces, the margins crenulate to entire; petioles short, 3–8 mm long, glabrous. *Inflorescences* in terminal and subterminal panicles, the flowers borne on dichotomously branched panicles, the peduncles puberulous; bracts oblanceolate to 7 mm long, 1 mm wide; pedicels mostly 5–10 mm long, glabrous. *Flowers* with calyx 5-merous, segments oblong, to 20 mm long, 3.5 mm wide, apically acute, glabrous; corolla white to pale yellow, to 6 cm long, glandular puberulous, tube to 3.5 cm long, 4.5 mm wide at base, narrowing above the ovary, expanding to 5 mm wide at the mouth, the lips to 2.5 cm long, the upper lip erect, to 8 mm wide, apically bidentate, the teeth ca. 1.5 mm long, the lower lip spreading, all the lobes oblong, the middle lobe to 6 mm wide, the lateral lobes 4.5 mm wide, all apically rounded; stamens exserted to near the apex of the upper lip, the anther cells superposed, the lower cell spurred. *Capsules* clavate, to 15 mm long, 5 mm broad, 4 mm thick, glabrous; seeds near spherical, 3.5 mm diameter, glabrous.

This species grows as a vine in lowland rain forest of Panama.

CANAL ZONE: Río Providencia, 3 km SE of Achiote near west border of Canal Zone, 5–100 m, *Gentry & Nee 8653* (MO). Río Providencia and ridge S of river, 5–170 m, *Gentry & Nee 8738* (MO). BARRO COLORADO ISLAND: *Brown 56* (F); *Busey & Croat 233* (DUKE); *Croat 7357, 7372, 8067, 12669* (all MO); *Foster 1432* (DUKE, MO); *Shattuck 602* (MO, US), *602a* (F, US); *Wetmore & Abbe 107* (F, MO). DARIÉN: Río Mortí, ca. 6 mi upstream from Mortí Abajo, ca. 100 m, *Duke 10165* (MO). PANAMÁ: Beyond Cerro Jefe, vicinity of "School House," *Dressler 3226* (MO). Majé, old forest, fairly flat, ca. 5 mi up the Río Nuevo, a main branch of the Río Majé, *Foster & Kennedy 1990* (DUKE). VERAGUAS: 5 mi W of Santa Fé on road past Escuela Agrícola de Alto Piedra on Pacific side of Divide, ca. 800–1200 m, *Croat 23087* (MO).

9. **Justicia macrantha** Benth., Pl. Hartw. 78: 1839. TYPE: Mexico, *Hartweg* (K, not seen).

Shrub to 3 m tall; stems terete, pilose to glabrate. *Leaves* elliptic, to 18 cm long, 6 cm wide, apically acuminate, basally attenuate, glabrous on both surfaces except for pilose hairs on the midrib in some, the margins crenulate; petioles to 1.5 cm long, pubescent as on the stem. *Inflorescences* in axillary cymes; bracts and bracteoles subulate, 2–2.5 mm long, 1 mm wide at the base, glabrous; rachises to 4 cm long, glabrous to sparingly pilose; pedicels 3–5 mm long, glabrous. *Flowers* with the calyx lobes subulate, 4–5 mm long, 1 mm wide at the base, slightly keeled, glabrous, sometimes ciliolate toward the base; corolla orange red to yellowish, to 5.5 cm long, deeply bilabiate, glabrous, the tube

funnelform, basally 4 mm wide, 7 mm wide at the mouth, both the lips ca. 2.8 cm long, the upper lip erect, 8 mm wide, apically dentate in 2 short lobes and hooded to enclose part of the style, the lower lip spreading, 1 cm wide, 3-lobed at the tip, the lobes about equal, 4 mm long, apically rounded; stamens exserted, the anthers pendulous, converging apically and diverging basally, the cells 2.5 mm long, slightly unequal, basally rounded, the filaments stout, 1 mm wide, glabrous. *Capsules* clavate, to 2.2 cm long, 4 mm wide, puberulous; seeds oval, flattened, 3 mm long, 2 mm wide, roughened.

This species occurs in moist forests of Central America. The opened flowers are said to resemble the mouth of a serpent. Capsule and seed descriptions were obtained from *Skutch 4693* (NY), El General, Costa Rica.

CHIRIQUÍ: Boquete District, 5000 ft, *Davidson 504* (F, MO). Río Chiriquí Viejo valley between El Volcán and Cerro Punta, *White 22* (MO). COCLÉ: El Valle de Antón, trails near Finca Tomas Arias, 600 m, *Allen 4226* (MO).

10. **Justicia metallica** Lindau, Pittier, Primit. Fl. Costaric. 2: 311. 1900. TYPE: Costa Rica, *Pittier 3497* (US, not seen).

Herb to 50 cm tall; stem ascending, rooting at the lower nodes, quadrangular when younger, the angles rounded, pilosulous in 2 lines, mixed with glandular hairs toward the apex, purplish. *Leaves* ovate, 3–9 cm long, 1.5–4 cm wide, apically acuminate to short acuminate, basally sparingly attenuate to rounded, glabrous to sparingly strigose along the midrib and the costa, the cystoliths prominent on both the surfaces, greenish above, shiny metallic blue beneath, the margins entire, undulate or crenate; petioles short, 3–8 mm long, strigose above. *Inflorescences* of lax, terminal or axillary, spicate panicles, the spikes to ca. 9 cm long, the first internode ca. 1 cm long, the peduncles and the rachises glandular puberulous, purplish; bracts and bracteoles linear subulate, to 1.5 mm long, 0.25 mm wide, glandular puberulous; pedicels secund. *Flowers* with the calyx 4-merous, the segments subulate, to 5 mm long, ca. 0.5 mm wide at the base, glandular puberulous; corollas pink to purplish, to 14 mm long, sparingly glandular puberulous, the tube cylindrical to 9 mm long, 2 mm wide, the upper lip erect, to 4.5 mm long, 2 mm wide, apically minutely bidentate, the lower lip spreading, to 5.5 mm long, the lobes to 2 mm long, the middle lobe 2 mm wide, the lateral lobes 1.5 mm wide, all apically rounded; stamens exserted to just below the tip of the upper lip, the anther cells superposed, ca. 1 mm long, the lower cell spurred. *Capsules* clavate, to 8 mm long, 1.5 mm wide, sparingly puberulous; seeds reddish brown, subtriangular, ca. 1 mm wide, roughened.

This species is found along stream banks and wet places of rain forests at lower elevations in Costa Rica and Panama.

BOCAS DEL TORO: Changuinola Valley, *Dunlap 381* (F, US). CANAL ZONE: Secondary forest, Ft. Sherman Road S-1 between Gatún and Piña, 0–170 m, *Liesner 1355* (MO). Forest between Peluca Hydrographic Station and Quebrada Peluca, along Río Boqueron, 70 m, *Steyermark & Allen 17241* (MO). CHIRIQUÍ: Burica Peninsula, Rabo de Puerco, 10.5 km W of Puerto Armuelles, in forest, 100 m, *Busey 517* (MO). Burica Peninsula, San Bartolo, 12 km W of Puerto Armuelles, 200 m, *Busey 711* (MO). COLÓN: Santa Rita Ridge E of Transisthmian Highway, 300–500 m, *Gentry 6556* (MO). DARIÉN: Near Refugio, 15–21 mi

N of Santa Fé, ca. 30 m, *Duke 10301* (US). PANAMÁ: Tributary of Río Chagres, 5 mi SW of Cerro Brewster, 1000 ft, *Lewis et al. 3407* (MO). Gorgas Memorial Labs yellow fever research camp, ca. 25 km NE of Cerro Azul on Río Piedras, 550 m, *Mori & Kallunki 3376* (MO).

11. **Justicia oerstedii** Leonard, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1938. Based on *Chiloglossa glabra* Oerst.

Chiloglossa glabra Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1854: 161. 1855. TYPE: Costa Rica, *Oersted* (not seen).
Dianthera glabra (Oerst.) Hemsley, Biol. Centr. Amer. Bot. 2: 518. 1882.
Justicia glabra (Oerst.) Lindau, in Pitt., Primit. 2: 312. 1900, not *J. glabra* Roxb. (1820).

Herb, sometimes suffrutescent to 1.5 m tall; stems erect, terete to subquadrangular when young, glabrous to puberulous. *Leaves* elliptic to ovate, to 10 cm long, 4.5 cm wide, apically acuminate to obtuse, basally attenuate, glabrous, the cystoliths visible on both the surfaces, the margins entire to slightly undulate; petioles short, to ca. 5 mm long, glabrous. *Inflorescences* in terminal, spicate panicles, to 20 cm long, the spikes lax, the peduncles and the rachises glandular puberulous; bracts and bracteoles narrowly subulate, 1–1.5 mm long, ca. 0.5 mm wide basally, puberulous. *Flowers* with 5-merous calyx, the calyx segments subulate, to 3.5 mm long, the posterior segment smaller, to 2 mm long, 1 mm wide basally, keeled, puberulous; corolla bright red, to 3 cm long, puberulous, the tube narrow, 1 mm wide basally, 5 mm wide at the mouth, the upper lip oblong, 9 mm long, 5 mm wide, apically minutely bidentate, the lower lip 10 mm long, 3-lobed, the middle lobe 2.5 mm wide, the lateral lobes 1.5 mm wide, all the lobes 3 mm long, apically rounded; stamens exserted to about the tip of the upper lip, the anther cells superposed by a connective 0.5 mm wide, the lower cell rounded, acute at the base. *Capsules* clavate, 12 mm long, 2 mm wide, puberulous; seeds suborbicular, flattened, ca. 1.5 mm in diameter, roughened.

This species is found in wet areas along streams, trails and in thickets and forests from 500 to 2,000 m in Costa Rica and Panama.

CHIRIQUÍ: Trail from Paso Ancho to Monte Lirio, upper valley of Río Chiriquí Viejo, 1500–2000 m, *Allen 1475* (MO). Bajo Mono, Boquete, 4500 ft, *Davidson 494* (MO). Wet slopes of Sierra del Boquete, 4500 ft, *Maurice 879* (US). Boquete, 1000–1300 m, *Maxon 2983* (US), *5005* (NY). Forests around El Boquete, 1000–1300 m, *Pittier 2983* (NY). Weedy roadside 4 mi NE of El Hato del Volcan towards Costa Rica and Cerro Pando, *Wilbur et al. 15325* (DUKE). COCLÉ: N rim of El Valle de Antón, 600–1000 m, *Allen 1672* (MO). El Valle de Antón, along Río Indio trail, 500–700 m, *Hunter & Allen 324* (MO). Hills NE of El Valle de Antón, 2000 ft, *Lewis et al. 1694* (MO). El Valle de Antón, 1840 ft, *Maurice 767* (US). COLÓN: Santa Rita Ridge, end of road from Transisthmian Highway, *Porter et al. 4754A* (MO). PANAMÁ: Campo Tres, 5 km NE of Altos de Pacora, *Busey 824* (MO). 5–10 km NE of Altos de Pacora on trail at end of road, ca. 750 m, *Mori & Kallunki 4988* (MO). Cerro Campana, above Su Lin Motel, *Porter et al. 4206, 4307* (both MO).

12. **Justicia panamense** Durkee[10]. TYPE: Panama, *Dwyer et al. 8213* (MO). —FIG. 17.

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[10] *Justicia panamense* Durkee, sp. nov. Herba vel suffrutex radicans, caulibus subteretibus glabris vel secus lineam unicam puberulis; folis ovatis, 5–9 cm longis, 1.5–4.0 cm latis, acuminatis, basim obtusatis vel rotundatis, glabris, cystolithis creberrimis sed obscuris; petiolis brevis, 3–5 mm longis; inflorescentis axillaribus, ex spicis solitariis vel geminis compactis, ad 6 cm longis, 4 mm latis constantibus; corolla alba puberula, ad 6 cm longa, staminibus longitudine labio supremo exsertis, cellulis antherarum superpositis, connectivo 3.5 mm lato.

Herb, sometimes suffrutescent with vinelike stems; stems subterete, glabrous to puberulous along one line. *Leaves* ovate, to 6.5 cm long, 2.5 cm wide, apically acuminate, basally obtuse to rounded, glabrous, the cystoliths numerous but obscure, the margins entire to undulate; petioles short, 3–5 mm long, pubescent as on the stem. *Inflorescences* in axillary spikes borne singly or in pairs, the spikes compact to 6 cm long, 1.5 cm wide, the rachis puberulous; bracts imbricate, elliptic to obovate, to 8 mm long, 4 mm wide, apically acute to obtuse, puberulous, ciliolate; bracteoles narrowly elliptic to oblanceolate, to 8 mm long, 2 mm wide, puberulous, ciliolate. *Flowers* with 5-merous calyx, the segments lanceolate, to 8 mm long, 2 mm wide, puberulous; corolla white, to 6 cm long, puberulous, the tube narrowly funnelform, to 4 cm long, 3 mm wide basally, narrowing above the ovary, expanding to 6 mm wide at the mouth, the upper lip erect, to 2 cm long, 10 mm wide, minutely bidentate apically, the lower lip spreading, ca. 18 mm long, 3-lobed, the lobes oblong, 10 mm long, apically rounded, the middle lobe 7 mm wide, the lateral lobes 5 mm wide; stamens exserted to the tip of the upper lip, the filaments glabrous, the anther cells superposed, connective 3.5 mm wide, the upper cell 4 mm long, basally acute, the lower cell 3 mm long, basally ending in a blunt tip; ovary glabrous. *Capsules* not observed.

This species has been found only in the type location. It was described by collectors as vinelike. The specimen was found in upland rain forests at just under 1,000 m.

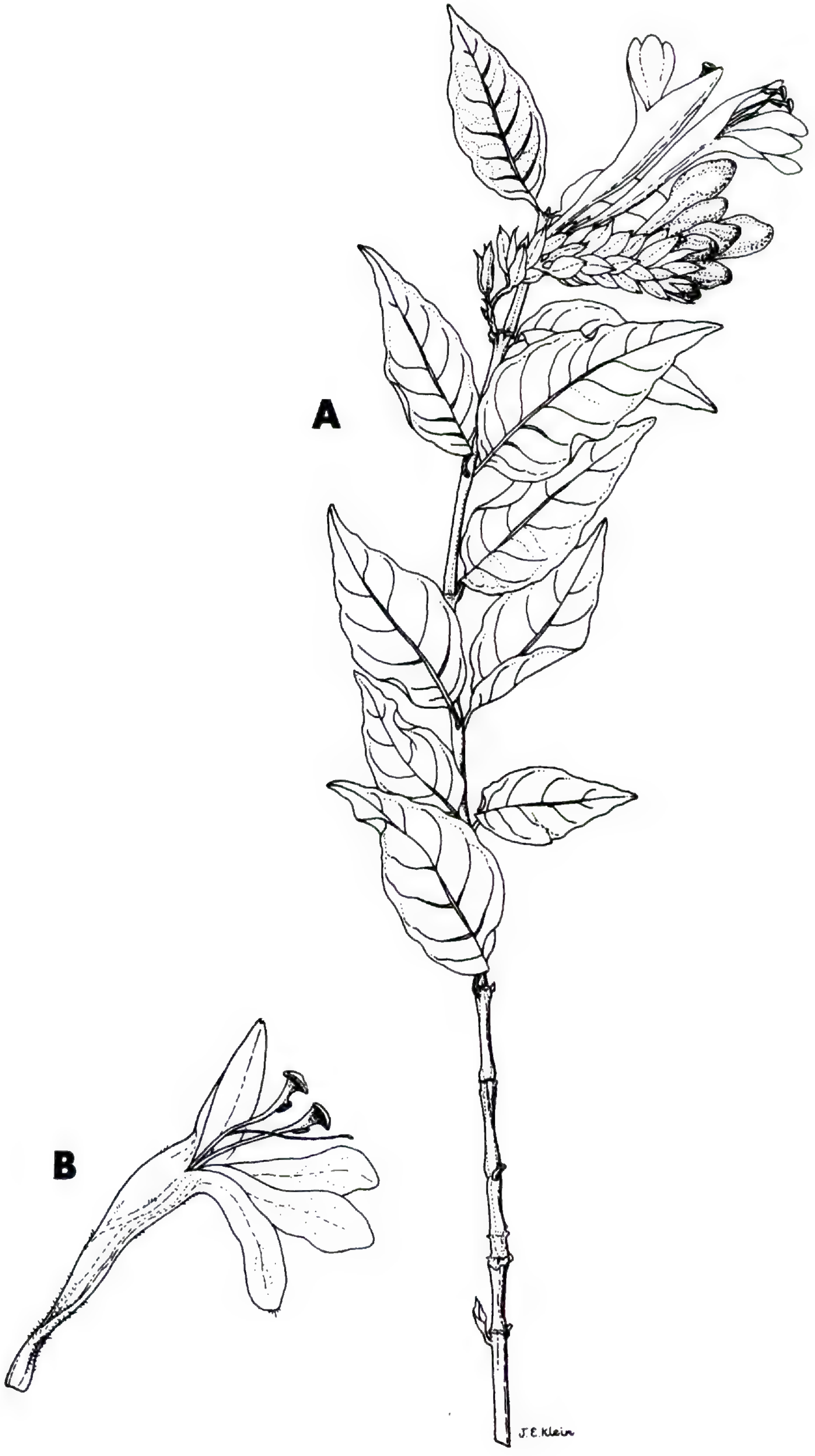
PANAMÁ: 2.4 mi beyond Cerro Jefe on road to Altos de Pacora, 800–1000 m, *Croat 22667* (MO). Cerro Jefe to La Eneida, to 2900 ft, *Dwyer et al. 8213* (MO). Cerro Jefe, ca. 1000 m, *Gentry 6761* (MO). Along small stream in premontane wet forest area 8.5 km by road NE of Lago Cerro Azul on road to Cerro Jefe, 800 m, *Hansen 3020* (MO). 5–10 km NE of Altos de Pacora ca. 15 km from Cerro Azul, *Mori et al. 4198* (MO). Slopes of Cerro Jefe between Cerro Azul and La Eneida ca. 15 mi NE of Panama City, *Wilbur et al. 15536* (DUKE).

13. **Justicia pectoralis** Jacq. Enum. Pl. Carib. 11. 1760. TYPE: Dominica, West Indies (not seen).

13a. **Justicia pectoralis** var. **pectoralis**

Dianthera pectoralis (Jacq.) Gmelin, Syst. Nat. 2: 36. 1791.

Herbs to 2 m tall; stems weak, erect or ascending, often rooting at the lower nodes, subquadrangular, grooved, glabrous to puberulous, the hairs retrorse. *Leaves* narrowly to broadly lanceolate, to 9.5 cm long, 2.5 cm wide, apically acuminate, basally acute to obtuse, the cystoliths dense and prominent above, not visible beneath, glabrous to strigose at the costa above, glabrous beneath, the margins entire to undulate; petioles short, to ca. 5 mm long, strigose above. *Inflorescences* in terminal, lax, spicate panicles to 25 cm long, 15 cm broad, the lower internodes of spicate branches ca. 2 cm long, the rachises and the peduncles glandular puberulous; bracts and bracteoles subulate, 2 mm long, 1 mm wide basally, puberulous and with a few glandular hairs. *Flowers* with 5-merous calyx, segments narrowly subulate, to 2 mm long, 0.5 mm wide basally, glandular puberulous; corollas white, lilac or purple, 8–12 mm long, puberulous outside, the throat transversely plicate, often spotted with dark purple, the tube nar-


A
B
J.E. Klein

rowly funnelform, basally 1.25 mm broad, 2.5 mm wide at the mouth, the upper lip erect, triangular, 3.5 mm long, 3 mm wide, apically acute, the lower lip spreading, to 5 mm long, 3-lobed, the lobes 1 mm long, the middle lobe 2 mm wide, the lateral lobes 1.5 mm wide, all apically obtuse; stamens exserted to about the tip of the upper lip, the anther cells slightly superposed, basally apiculate, the filaments glabrous. *Capsules* clavate, to 8 mm long, 2 mm wide, puberulous; seeds orbicular, flattened, 1.5 mm in diameter.

This species is a common weed of roadsides and waste places at elevations near sea level in tropical America and the West Indies.

CANAL ZONE: Roadside Madden Forest Road 1, *Croat 8935* (MO). Ancón, near Gorgas Hospital, *Croat* 9235 (MO). BARRO COLORADO ISLAND: *Croat 10253* (MO). Summit Garden, *Croat 12831* (MO). Forest along banks of Quebrada La Palma and Cañon or Río Chagres, 70–80 m, *Dodge & Allen 17402* (MO). Albrook, U.S. Army Tropic Test Center Site, *Dwyer & Robyns 51* (MO). Balboa Heights, *Greenman & Greenman 5076* (MO). ½ mi S of Gamboa along Chagres, *Lazor 2280* (MO). Boy Scout Road, Madden Dam area, second growth forest, *Porter et al. 4028A* (MO). Pueblo Nuevo, *White 298* (MO). CHIRIQUÍ: 12.4 mi N of Davíd, edge of steep river bank, *Lewis et al. 723* (MO). COLÓN: Juan Mina Plantation, Río Chagres, Region above Gamboa, 25 m, *Allen 4112* (MO). DARIÉN: Manene to mouth of Río Cuasi, *Kirkbride & Duke 1526* (MO). Camp Summit, Darién-San Blas border along Sea Level Canal Rt. 17, 1000–1200 ft, seasonal evergreen forest and weedy clearing, *Oliver et al. 3665* (MO). PANAMÁ: Hills between Capira and Potrero, 80–130 m, *Dodge & Hunter* (MO). Chimán, rocky beach, *Lewis et al. 3365* (MO).

13. **Justicia pectoralis** Jacq. Durkee[11]. TYPE: Panama, *Duke 10028* (MO).

13b. **Justicia pectoralis** var. **macrophyllus**

Variety *macrophyllus* differs from the typical *J. pectoralis* principally in the elliptic to obovate leaves. The leaves are also larger, to 18 cm long, 7.5 cm wide, and the branches of the inflorescences lack glandular hairs with pubescence restricted to 2 sparingly strigulose lines.

DARIÉN: Summit Camp, ca. 400 m between Sasardí and Mortí, *Duke 10028* (MO). Camp Summit, Darién-San Blas border along Sea Level Canal Rt. 17, 1000–1200 ft, seasonal evergreen forest and weedy clearing, *Oliver et al. 3665* (MO).

14. **Justicia refractifolia** (Kuntze) Leonard, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1938.

Echolium refractifolium Kuntze, Rev. Gen. Pl. 2: 487. 1891. TYPE: Costa Rica, *Kuntze* (not seen).

Justicia pseudopolystachya Cuf., Archivo Bot. 10: 49. 1934. SYNTYPES: Costa Rica, *Cufondontis 349 & 652* (neither seen).

Herb, sometimes suffrutescent to 1 m tall; stems erect, simple, subquadrangular toward the apex, subterete below, pilose. *Leaves* elliptic, to 18 cm long,

[11] *Justicia pectoralis* var. *macrophyllus* Durkee, var. nov. Differt ab varietate typica foliis ellipticis vel obovatis, grandioribus, ad 18 cm longis, 7.5 cm latisque, ramis inflorescentiae sine pilis glandulosis indumento non nisi ex lineis duo sparsim strigulosis constanti.

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FIGURE 17. *Justicia panamense* Durkee.—A. Habit (×⅗).—B. Corolla (×⁹⁄₁₀). [After *Dwyer et al. 8213* (MO).]

7 cm wide, apically acuminate, basally acute to attenuate, glabrous to strigose along the costa and the veins above, pilose beneath, the margins entire to undulate; petioles 5–15 mm long, pilose. *Inflorescences* in terminal and axillary spikes, borne singly and in clusters, to 15 cm long, 1 cm wide, the rachis pilose to strigose; bracts ovate, to 10 cm long, 6 cm wide, imbricate, apically acute, drying brown, the veins prominent, pilose both surfaces, ciliate; bractlets lanceolate, falcate, to 8 mm long, 2.5 mm wide, ciliolate. *Flowers* with 5-merous calyx, segments narrowly subulate, to 6 mm long, 0.5 mm wide, ciliate; corollas white to purple, to 11 mm long, puberulous, the tube cylindrical, 7 mm long, 1.5 mm broad, the upper lip erect, 4 mm long, 2 mm wide, apically bidentate; lower lip 4 mm long, 3-lobed, the lobes 2.5 mm long, apically obtuse, the middle lobe 2.5 mm wide, the lateral lobes 2 mm wide; stamens exserted to about the notch of the upper lip, the filaments attached just below the throat, pubescence of minute glandular hairs, the anther cells superposed; the lower cell spurred. *Capsules* clavate, 9 mm long, 2 mm broad, puberulous; seeds subtriangular, ca. 1.5 mm across, flattened, reddish brown, roughened.

This species is found in rain forests at lower elevation in Costa Rica and Panama.

BOCAS DEL TORO: Punta Pena, near Chiriquicito, ca. 1000 ft, *Lewis et al. 2164* (MO). Chiriquí Lagoon, *Wedel 143* (MO), *1571* (MO, US). Isla Colon, ca. 25–75 m, *Woodson et al. 1935* (MO). COLÓN: Santa Rita Ridge Road, 4 mi from Transisthmian Highway to Agua Clara weather station, ca. 500 m, *Dressler et al. 8860* (MO). Santa Rita Ridge E of Transisthmian Highway, 300–500 m, *Gentry 6584* (MO). Road into Santa Rita, E of Agua Clara rain gauge, *Kennedy 2748* (MO). 2–3 mi up the Río Guanche, lowland rain forest, ca. 10–20 m, *Kennedy & Foster 2161a* (MO). Santa Rita Ridge, end of road from Transisthmian Highway, ca. 10 mi from highway, *Porter et al. 4751, 4770* (both MO). DARIÉN: Boca de Pauarando, on Sambú River, 20 m, *Pittier 5589* (NY, US). PANAMÁ: El Llano-Carti Road, 10 km from Interamerican Highway, *Mori & Kallunki 2309* (MO). SAN BLAS: Trail E of Cangandi-Mandinga airport road, 2–5 mi S of airport, *Duke 14798* (US).

15. **Justicia secunda** Vahl, Symb. Bot. 2: 7. 1791. TYPE: Trinidad, *Rohr* (not seen).—FIG. 18.

Rhytiglossa secunda (Vahl.) Nees in DC., Prod. 11: 340. 1847.

Herb, sometimes suffrutescent, to ca. 2 m tall; stems subquadrangular when young, sparingly strigose. *Leaves* ovate to lanceolate, to 16.5 cm long and 6.5 cm wide, apically acuminate, basally acute or obtuse, the cystoliths numerous and prominent to ca. 2 mm long, glabrous to sparingly strigose on the costa, the margins entire to crenulate; petioles to 3 cm long, strigose to glabrous. *Inflorescences* thyrsoid to paniculate, mostly terminal, 5–15 cm long, 7 cm broad; rachis with the peduncle and the pedicel pilose, or with retrorse pubescence; bracts linear to subulate, to ca. 6 mm long and 0.5 mm wide, keeled, ciliolate; bracteoles 2, mostly linear to ca. 3 mm long, keeled, ciliolate; lower bracts longer and narrower, the upper bracts and the bractlets more triangular and shorter; pedicels secund. *Flowers* with the calyx 5-merous, the segments elliptic oblong, equal, to 9 mm long, 2 mm wide, apex acuminate, 3-nerved, glandular puberulous outside, glabrous inside, ciliolate; corolla red or purplish red, bilabiate, 2.5–4.3 cm long, the tube short, ca. 1 cm long, 3 mm wide at

FIGURE 18. *Justicia secunda* Vahl. Habit (×½). [After *Kennedy* 2880 (MO).]

base, 5 mm wide at the throat, puberulous glandular outside, the upper lip to 32 mm long and 8 mm wide with two small 1 mm wide, acute lobes at the apex, the lower lip slightly longer, to 35 mm long and 6.5 mm wide with 3 small, ca. 2 mm long, semiorbicular lobes at the apex, the middle lobe 2 mm wide, the lateral lobes 1.5 mm wide; stamens extending about as far as the upper

lip and mostly within it, the anthers usually exposed at maturity, the cells subparallel, attached unequally by a connective 0.5–0.75 mm wide, the upper anther cell 2 mm long, both cells ca. 0.5 mm broad, filaments glabrous, flattened; style held within the upper lip, extending just beyond the stamens, increasingly puberulous toward the tip, the stigma subcapitate. *Capsule* clavate, ca. 1 cm long, 5 mm wide, the apex acute, minutely puberulous; seeds 4, semiorbicular, ca. 3 mm in diameter with a thin winged rim extending out 0.5 mm.

This species is found in forests and along streams in the West Indies, Panama, and Colombia.

BOCAS DEL TORO: Chiriquicito to 5 mi S along Río Guarumo, *Lewis et al. 2066* (MO). CANAL ZONE: Fort Kobbe, *Allen 2029* (MO). Madden Forest Road 2 along stream, *Croat 8962* (MO). Pipeline Road 2½ mi from Gamboa gate, *Croat 9351* (MO). Road C-16 NW of Pedro Miguel, *Croat 12259* (MO). Westerly arm of Quebrada Salamanca, 70 m, *Dodge et al. 16986* (MO). Forest along banks of Quebrada Fea, Quebrada Pura and Cañon of Río Chagres, 70–100 m, *Dodge & Allen 17424* (MO). Frijoles, *Ebinger 621* (F). Old Gamboa Road near Summit Hills golf course, *Gentry 1458A* (MO). Road C-29 beyond Summit, *Harvey 5217* (F). Madden Dam, 50 ft, *Lewis et al. 32* (MO). *Lewis et al. 5301* (MO). Juan Mina, *Piper 5695* (F). Casa Larga, drowned forest and sabanas on banks of Quebrada Melgada, 70–75 m, *Steyermark* (MO). 6 mi N of Gamboa, *Tyson 3497* (MO). COCLÉ: N rim of El Valle de Antón, 600–1000 m, *Allen 1673* (NY). Ca. 39 km from Interamerican Highway, *Correa 334* (DUKE, MO). Between Cerro Pilon and El Valle de Antón, 700–900 m, *Duke & Dwyer 13973* (MO). El Valle, *Dwyer 1832* (MO). Above El Valle, *Gentry 5622* (MO). Along road and in cloud forest 5 mi N of El Valle de Antón, ca. 1000 m, *Luteyn 1200* (DUKE). El Valle de Antón, 500–700 m, *Seibert 431* (MO). Road from El Valle to La Mesa, 2500 ft, *Tyson et al. 3970* (MO). La Mesa, above El Valle de Antón, 1000 m, *Weaver & Foster 1630* (DUKE). COLÓN: 6 mi S of Portobelo, *Croat 11409* (MO). Río Iguanitos, *Elias & Kirkbride 1637* (MO). Stream ca. 3 mi E of Transisthmian Highway on road to Salamanca, ca. 100 m, *Gentry 6725* (MO). Near Peluca, secondary vegetation along Río Boqueron, *Kennedy 2811* (MO). Flood plain, 3 mi E of Portobelo, ca. 20 m, *Liesner 1108* (DUKE, MO). In limestone stream, Rosario road near Gatuncillo, *Smith et al. 3325* (F). DARIÉN: 4 mi up Río Sabana from Santa Fé, *Duke 4133* (MO). Río Sabana above Santa Fé, *Duke 14109* (MO). Río Pirre, trail upriver from house of Bartolo, *Kennedy 2880* (MO). Village of Manene, *Kirkbride & Bristan* 1628 (MO). HERRERA: Banks of Río Santa Maria, *Burch et al. 1192* (MO). PANAMÁ: 1.5 mi above Interamerican Highway on road to Cerro Campana, *Croat 12036* (MO). Bald savannalike areas toward top of Cerro Campana, *Duke 5984, 5984A* (both MO). Isla del Rey, *Duke 9569* (MO). Near confluence of Río Pacora and Río Corso, 450 m, *Duke 11975* (MO). Piria-Canasas trail near Piria, ca. 100 m, *Duke 14340* (DUKE). Capira, along trail between Lidice and Aguacate, 300 m, *Foster 2136* (DUKE). Majé, old forest, fairly flat, ca. 5 mi up the Río Nuevo, *Foster & Kennedy 1989* (DUKE). Natural bridge, in stream bed, *Gentry 5613* (MO). Between Chepo and El Llano, *Gentry 6456* (MO). La Mesa (Pacora), *Herrera 12* (DUKE). 5 mi W of Chepo near the Interamerican Highway, *Tyson 6730* (MO). Juan Diaz, *Vergara 16* (DUKE). PROVINCE UNKNOWN: *Duke 6149* (MO).

16. **Justicia tinctoria** (Oerst.) D. Gibson, Fieldiana, Bot. V. 34, no. 6. 74. 1972.

Sericographis tinctoria Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1854: 150. 1855. TYPE: Costa Rica, *Oersted* (not seen).
Jacobinia tinctoria (Oerst.) Hemsley, Biol. Centr. Amer. Bot. 2: 552. 1882.

Shrubs to 2 m tall; stems subquadrangular, the angles rounded, glabrous to sparingly pilose. *Leaves* ovate lanceolate, to 17 cm long, 5.5 cm wide, apically acuminate, basally attenuate, the cystoliths dense, more visible on the upper surface, glabrous on both surfaces, the margins entire, ciliolate; petioles to 1 cm long, pubescent as on the stem. *Inflorescences* in lax axillary, spicate panicles

with secund flowers, the spikes to 4 cm long, peduncles to 3.5 cm long, glabrous; rachis quadrangular, glabrous, internodes 4–5 mm apart; bracts and bracteoles triangular subulate, 1–2 mm long, 0.5–1 mm wide at the base, ciliolate. *Flowers* with 5-merous, triangular subulate calyx segments, 2.5–3 mm long, 1 mm wide at the base, glabrous; corolla orange or red, to 4 cm long, glabrous, the tube slightly funnelform, 3 mm wide at the base, 5 mm wide at the mouth, the lips subequal, ca. 16 mm long, the upper lip ovate, erect, 7 mm wide at base, apically acute and keeled, the lower lip oblong, erect or slightly spreading, 4.5 mm wide, apically 3-lobed, the lobes equal, 2 mm long, 1 mm wide, apically obtuse and keeled; stamens exserted to about the tips of the lips, the anther cells slightly subequal, 2.5 mm long, obliquely attached to the connective, mucronulate, basally acute, the filaments glabrous. *Capsules* not seen.

Found in dry thickets of Central America, this plant is often cultivated. The leaves when treated with hot water give a blue solution used by laundresses as bluing for white clothes.

CHIRIQUÍ: Foot of Cerro Horqueta, Boquete, 3500 ft, *Maurice* 868 (US). DARIÉN: Quebrada "Camachimuricate" casa de Bartolo, *Kennedy 2830* (MO). PANAMÁ: Bohio Soldado, *Cowell* 246 (NY). Cerro Jefe, main road before turnoff to summit, *Croat 13030* (MO). El Llano-Carti Road, 9.6–11 km from Interamerican Highway, wet forest, 1100–1200 ft, *Mori & Kallunki 3515* (MO). NE of Cerro Azul, 20 km by road from Interamerican Highway, *Mori & Kallunki 3648* (MO).

17. **Justicia trichotoma** (Kuntze) Leonard, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1236. 1938.

Ecbolium trichotomum Kuntze, Rev. Gen. Pl. 2: 488. 1891. TYPE: Costa Rica, *Kuntze* (not seen).

Justicia asymetrica Lindau in Pittier, Primit. Fl. Costaric. 2: 310. 1900. TYPE: Costa Rica, *Biolley 7383.*

Shrubs to 1.5 m tall; stems erect, subquadrangular, the lower portions terete, strigose. *Leaves* ovate to ovate lanceolate, one blade of each pair conspicuously larger than the other, the larger blade to 11 cm long, 4 cm wide, the smaller blade to 6.5 cm long, 2.5 cm wide, all apically acuminate, basally attenuate, sparingly strigose above, pubescence mostly restricted to the costa, the lower surface similar, but more pubescent, the cystoliths inconspicuous, visible on the lower surface only, the margins undulate; unwinged portions of petiole to 1 cm long, strigose. *Inflorescences* in small axillary cymes, the peduncles to 2.5 cm long, strigose; bracts and bracteoles subulate, to 1.5 mm long, 0.5 mm wide basally, strigose. *Flowers* sessile, calyx 5-merous, the segments narrowly subulate, to 6 mm long, 1 mm wide, puberulous; corolla violet, to 2 cm long, puberulous, the tube funnelform, 1.5 mm wide basally, 4 mm wide at the mouth, the upper lip 6 mm long, 4 mm wide, apically acute, the lower lip 7 mm long, 3-lobed, the lobes 3 mm long, apically obtuse, the middle lobe 2.5 mm wide, the lateral lobes 2 mm wide; stamens exserted to about the tip of the upper lip, the anther cells superposed, the lower cell calcarate. *Capsules* clavate, to 10 mm long, 2 mm wide, 1 mm thick, puberulous; seeds dark brown, suborbicular, ca. 2 mm in diameter, roughened.

This species grows in wet thickets, adjacent to streams and clearings and is found in rain forests of Costa Rica and Panama.

BOCAS DEL TORO: Region of Almirante, *Cooper 126* (NY). DARIÉN: 400 m, between Sasardí and Mortí, *Duke 10044* (MO). Darién-San Blas border along Sea Level Canal Rt. 17, 1000–1200 ft, seasonal evergreen forest and weedy clearing, *Oliver et al. 3672* (MO). SAN BLAS: Darién-San Blas border, Helipad in Premontane rain forest, ca. 1200 ft, *Duke 15484* (US).

18. **Justicia urophylla** (Lindau) D. Gibson, Fieldiana, Bot. 34: 74. 1972.

Belaperone urophylla Lindau in Pittier, Primit. Fl. Costaric. 2: 315. 1900. TYPE: Costa Rica, *Tonduz 4077* (B?, not seen).

Shrub to 2 m tall; stems subterete, glabrous to sparingly puberulous in 2 lines. *Leaves* ovate elliptic, to 17 cm long, 6.5 cm wide, apically acuminate, basally attenuate, glabrous, the cystoliths dense, plainly visible on both the surfaces, the margins entire to undulate; petioles 1–2 cm long, pubescent as on the stem. *Inflorescences* in one to several dense spikes to 6 cm long, ca. 6 cm wide, the peduncles to 2 cm long, puberulous in 2 lines, the rachis glabrous to puberulous; bracts linear subulate, to 7 mm long, ca. 1 mm wide at the base, puberulous, ciliolate, the bracteoles triangular, ca. 1 mm long, 0.5 mm wide at base, puberulous. *Flowers* imbedded in the rachis, the calyx segments 5, equal, subulate, to 3 mm long, 1 mm wide at base, puberulous; corolla white, to 4.0 cm long, puberulous, the tube slightly funnelform, 2 mm wide at the base, slightly narrower above the ovary, 3 mm wide at the mouth, the lips to 16 mm long, the upper lip erect, apically bidentate, the lower lip 3-lobed, each lobe 1 cm long, the middle lobe 4 mm wide, the lateral lobes 3 mm wide, all apically rounded; anther cells superposed, spurred connective ca. 1 mm long, the filaments glabrous. *Capsules* clavate, to 16 mm long, 4 mm wide, glabrous; seeds orbicular, flattened, light brown, ca. 3 mm in diameter, glabrous.

This species is found in lowland rain forests of Costa Rica and Panama.

CHIRIQUÍ: Burica Peninsula, Corotú, 6 km SW of airport of Puerto Armuelles, *Busey 397* (MO). Secondary forest along Quebrada Punta de Piedra, 2 mi SW of Puerto Armuelles, 0–100 m, *Croat 22439* (MO). Stream, remnant forest in pasture, Quebrada Mellize, 6 mi S of Puerto Armuelles; 0–150 m, *Liesner 433* (MO). VERAGUAS: Continental Divide, third branch of Río Santa Maria to dropoff to lowlands, 12–15 km NW of Santa Fé, 650–750 m, *Dressler 4861* (MO).

18. KALBREYERIELLA

Kalbreyeriella Lindau, Notizbl. Bot. Gart. Berlin-Dahlem 8: 143. 1922. TYPE: *K. rostellata* Lindau.

Herbs or *shrubs*. *Leaves* petiolate. *Inflorescences* in spikes, racemes or narrow panicles; bracts or bractlets shorter than the calyx. *Flowers* with the calyx 5-merous, deeply segmented, the segments lanceolate; corolla broad tubular, slightly gibbous, scarlet, glabrous or hirtellous, beaked at the tip before expansion of the lips, the upper lip erect, narrow, partially enclosing the stamens and the style, the lower lip triangular, recurved, the apex minutely trilobate;

stamens 2, exserted; anthers 1- or 2-celled; ovary glabrous; mature capsules not seen.

The three species described for this genus have been collected only in Colombia and Panama. *Kalbreyeriella* most closely resembles the genus *Razisea*, Oerst., but can be distinguished from it by its calyx lobes which are 2–3 times longer than the bracts and the bractlets, and by its corollas which are apically beaked prior to expansion.

1. **Kalbreyeriella rostellata** Lindau, Notizbl. Bot. Gart. Berlin-Dahlem 8: 143. 1922. TYPE: Colombia, *Kalbreyer 1524* (B? if extant, photo MO).—FIG. 19.

Herbs to *subshrubs;* stems erect, terete to subquadrangular, glabrous to puberulous. *Leaves* ovate elliptic to elliptic, 11.5–26 cm long, 4.5–10 cm wide, apically acuminate, basally attenuate, glabrous to subglabrous, the costa and the lateral veins moderately prominent (10–11 pairs), the cystoliths dense and conspicuous above, the margins entire; petioles to 2.5 cm long, glabrous. *Inflorescences* in loose terminal and axillary spikes, to 17 cm long, the peduncles to ca. 3 cm long, quadrangular, puberulous, the rachis quadrangular, puberulous, one bract subtending each flower, the bracts lanceolate, 5.5–6 mm long, ca. 1.5 mm wide, glabrous, the margins ciliolate. *Flowers* sessile to subsessile, the calyx segments subequal, lanceolate, 13–15 mm long, 2–3 mm wide, glabrous; corolla scarlet, to 5.5 cm long, glabrous to sparingly puberulous toward the tip, the tip curved outward before expanding, the tube ca. 2.5 mm wide at base, expanding abruptly to 12 mm at the middle and reduced to 10 mm at the mouth, the upper lip lanceolate, acute, to 13 mm long, 4 mm wide at base, erect in expanded flowers, the lower lip triangular, recurved, 13 mm wide at the base, apically 3-lobed, the lobes ca. 1 mm long, 0.5 mm wide; stamens attached near the base of the corolla tube, exserted ca. 20 mm beyond the mouth of the corolla tube to just beyond the tip of the upper lip which partially encloses them, the anthers 1-celled, 4 mm long, 1 mm wide, apically and basally acute, glabrous, the filaments glabrous. *Capsule* not seen.

This species is found along streams and trails in wet areas of rain forests at elevations of 100–1,600 m in Panama and Colombia.

COLÓN: Near stream in forest, Río Iguanita, *Dressler 4942* (MO).

19. LOUTERIDIUM

Louteridium S. Watson, Proc. Amer. Acad. Arts 23: 284. 1888. TYPE: *L. donnell-smithii* S. Watson.

Shrubs. Leaves petiolate, glabrous, the cystoliths present, the margins entire or crenate. *Inflorescences* in terminal panicles or racemes; bracts small. *Flowers* with 3-merous calyx; corolla large, red, light green or yellow, the tube expanding abruptly just above the ovary into a hood with 5 short, unequal lobes; stamens 2 or 4, exserted from an arched position in the bud, the anther cells parallel; style exserted from an arched position in the bud. *Capsule* sessile.

Five species are found in the wet forests of Mexico and Central America.

FIGURE 19. *Kalbreyeriella rostellata* Lindau. Habit (×⅗). [After *Dressler 4942* (MO).]

1. **Louteridium costaricense** Radlk. and Donnell Smith, Bot. Gaz. (Crawfordsville) 37: 422. 1904. TYPE: Costa Rica, *Tonduz 8123* (not seen).—FIG. 20.

Shrub to 1.5 m tall, glabrous. *Leaves* elliptic, to 32 cm long and 15 cm wide, apically acuminate, basally attenuate, membranous, the cystoliths dense and prominent on both the surfaces, glabrous, the margins entire. *Inflorescences* in terminal, narrow panicles, the peduncles to ca. 15 cm long, the bracts and the bracteoles ovate lanceolate, 8–12 mm long. *Flowers* with pedicels 1.5–3 cm long; sepals 3, elliptic 2–4 cm long, 2 cm wide, acute, containing numerous cystoliths, the venation conspicuous; corolla pale green or yellow; stamens 2.

This species is found in lowland rain forests.

BOCAS DEL TORO: Fish Creek Mountains, Chiriquí Lagoon, *Wedel 2283* (MO). CANAL ZONE: Miraflores Lake, *White 277* (MO). COCLÉ: El Valle, wet ditch bank in shade, *Tyson et al. 2464* (US). COLÓN: 2–3 mi up the Río Guanche, 10–20 m, *Kennedy & Foster 2180* (MO). DARIÉN: Pinogana, ca. 20 m, *Allen 918* (MO). HERRERA: Banks of Río Santa Maria, *Burch et al. 1189A* (MO). 4 mi S of Las Pozas, *Tyson 2667* (MO). LOS SANTOS: 12 mi S of Macaracas in creek, *Tyson et al. 3067* (MO). PANAMÁ: Juan Diaz, *Standley 30540* (US). SAN BLAS: El Llano-Carti highway, ca. 23 km N of El Llano, area of Panama-San Blas border, *Dressler 4310* (DUKE, MO).

20. MEGASKEPASMA

Megaskepasma Lindau, Bull. Herb. Boissier 5: 666. 1897. TYPE: *M. erythrochlamys* Lindau.

Shrubs. Leaves large, elliptic, lacking cystoliths, petioled. *Inflorescences* in loose, terminal spikes, the bracts and the bractlets large and conspicuously colored. *Flowers* with calyx of 5 equal segments; corolla bilabiate, salverform, the upper lip bifid, the lower lip 3-lobed; stamens 2, the anthers 2-celled; stigma subcapitate; capsules clavate, 4-seeded, the seeds borne on hooklike funicles.

This genus is monotypic and is endemic to the neotropics.

1. **Megaskepasma erythrochlamys** Lindau, Bull. Herb. Boissier 5: 666. 1897. TYPE: Venezuela, *Funk & Schlim 1171* (B? if extant, not seen).

Shrub to 4 m tall; stems subquadrangular, sparingly puberulous. *Leaves* elliptic, to 24 cm long and 10.5 cm wide, apically acuminate with a rounded, apiculate tip, basally acute, sparingly strigose on the costa and the lateral veins of both surfaces, the cystoliths none, the margins entire to crenulate; petioles puberulous, to 2 cm long. *Inflorescences* in clustered, loose, terminal spikes, the spikes to 19 cm long and 4 cm wide, the peduncle brown puberulous, to 3.5 cm long, the rachis brown puberulous, terete, the bract solitary, ovate to elliptic, to 3.5 cm long, 2 cm wide, apically acute, basally acute, deep red, drying to reddish brown, sparingly strigulose on both surfaces, mostly restricted to the costa, the margins entire; bractlets elliptic, to 20 mm long, 5 mm wide, apically acute, basally attenuate, sparingly strigulose. *Flowers* with the calyx segments equal, lanceolate, to 10 mm long, 2 mm wide at base, densely strigose; corolla white, tube cylindrical, to 25 mm long, 2 mm wide, pilosulous, the upper lip lanceolate,

FIGURE 20. *Louteridium costaricense* Radlk. & Donnell Smith. Habit (×½). [After *Dressler 4310* (MO).]

to 35 mm long, 5 mm wide basally, apically bilobed, the lobes subulate, 1.5 mm long, 0.5 mm wide at the base, the lower lip elliptic, 35 mm long, 8 mm wide, pilosulous outside, apically 3-lobed, the lobes lanceolate, 7 mm long, 2 mm wide at base; stamens exserted ca. 3 cm beyond throat of the corolla, the filaments glabrous, the anthers 4.5 mm long, 1.5 mm wide, basally mucronate; ovary 2

mm long, glabrous; capsules clavate, to 30 mm long, 8 mm wide, apically attenuate and mucronate, glabrous; seeds 4, suborbiculate, flattened, ca. 6 mm in diameter, glabrous.

This plant is native to Venezuela and is found cultivated throughout much of the neotropics. Capsules and seeds were described from a Costa Rican specimen, *Durkee 75-189* (MO).

CHIRIQUÍ: Cultivated at Motel Calejón, David, *D'Arcy 9759* (MO).

21. MENDONCIA

Mendoncia Vell., Vandl. Fl. Lusit. Bras. 43. 1788. TYPE: *M. aspera* Ruiz & Pavón (Peru).

Mendozia Ruiz & Pavón, Fl. Peruv. Chil. Prodr. 89. 1794.
Mendocia Spreng., Syst. 2: 765. 1825.
Engelia Karst. ex Nees in DC., Prodr. 11: 721. 1847.
Mendoncala Post & Kuntze, Lex. Gen. Phan. 360. 1903.

Tall, suffrutescent *vines*. *Leaves* opposite, petioled, entire, pinnately veined. *Flowers* axillary, 1 to several or occasionally many in each axil, each flower pedicillate and subtended by 2 flat or keeled bracts; calyx reduced to an annular, often membranous structure, usually glabrous; corolla equally 5-merous, tubular or funnelform, usually expanded at the base, the lobes reflexed or spreading; stamens 4, included, didynamous, the filaments short, the anthers linear lanceolate, usually flattened, apically acute, glandular puberulous, basally lobed, the lobes more or less unequal; ovary oblique. *Fruit* a compressed drupe, often oblique at the tip, the endocarp pulpy; seeds 1 or 2.

According to Leonard (1951) there are over 90 species described for this genus, all endemic to tropical America. The genus takes its name from Cardinal Mendonca, a Patriarch of Lisbon, Portugal.

a. Corolla 1.5 cm long; flowers in axillary umbels ..... 1. *M. brenesii*
aa. Corolla 2.5 cm long or more; flowers axillary, borne singly or in 2s or 3s.
  b. Stems glabrous or strigose, the hairs when present upwardly appressed.
    c. Stems narrowly winged; corolla over 3.5 cm long ..... 8. *M. retusa*
    cc. Stems not winged; corollas under 3.5 cm long.
      d. Bracts obovate; petioles 2–4 cm long ..... 3. *M. costaricana*
      dd. Bracts ovate to elliptic; petioles 1–2 cm long.
        e. Bracts hirsute, the hairs spreading; hairs of lower leaf surface chiefly confined to the costa and the veins ..... 7. *M. litoralis*
        ee. Bracts strigose to sericeous, the hairs appressed; hairs of the lower leaf surface evenly distributed ..... 4. *M. gracilis*
  bb. Stems pilose, the hairs spreading or retrorse.
    f. Bracts under 2.5 cm long; petioles less than 1 cm long ..... 5. *M. hirsuta*
    ff. Bracts to 4 cm long; petioles more than 1.5 cm long.
      g. Leaves with cordate bases; hairs on the upper leaf surface lacking stellate bases ..... 2. *M. cordata*
      gg. Leaves not cordate at base; hairs on the upper leaf surface with stellate bases.
        h. Bracts oblong lanceolate, widest below the middle, apically acuminate; hairs on stem evenly distributed, somewhat appressed ..... 6. *M. lindavii*
        hh. Bracts oblong elliptic, widest at the middle, apically rounded, hairs on stem mostly at the angles and spreading ..... 9. *M. tonduzii*

1. **Mendoncia brenesii** Standley & Leonard, Field Mus. Nat. Hist., Bot. Ser. 5. 18: 1239, 1937–38. TYPE: LaPalma de San Ramon, Costa Rica, *Brenes 6269* (F, not seen).

Stem a suffrutescent *vine*, scandent, subquadrangular, grooved, glabrous to sparingly and minutely strigose. *Leaves* elliptic to 12 cm long, blunt tip with a mucro 1–2 mm long, basally rounded, glabrous except for sparingly and minutely strigose on the costa, the margins entire; petioles to 2.5 cm long, sparingly strigose. *Flowers* in axillary umbels of 5–10 flowers, radiating from short, flat, rounded, axillary spurs; pedicels ca. 1 cm long, sparingly strigose; bracts ovate, to 14 mm long, 7 mm wide, the apex acuminate, the base rounded sparingly strigose without; corolla white, to 1.5 cm long, glabrous, the tube ca. 8 mm long and 3 mm in diameter, slightly expanded at the base, the lobes obcordate, ca. 7 mm in diameter; stamens included, the filaments ca. 1.5 mm long.

This species is distinguished by its axillary umbels of small, white flowers and is found in Costa Rica and adjacent regions of Panama.

CHIRIQUÍ: Casita Alta, Volcán de Chiriquí, 1500–2000 m, *Woodson et al. 989* (MO).

2. **Mendoncia cordata** Leonard, Contr. U.S. Natl. Herb. 31: 16–18. 1951. TYPE: El Valle, Colombia, *Cuatrecasas 15216* (US, not seen).

Suffrutescent *vine* with subquadrangular stem, densely pilose, hairs spreading, golden brown, to 3 mm long. *Leaves* ovate elliptic, to 15 cm long and 9 cm wide, apically acuminate or caudate, basally cordate, densely brown pilose on both the surfaces, the hairs ascending, ca. 2 mm long, the costa and the lateral veins especially prominent beneath, the veinlets forming coarse, conspicuous reticulations beneath, the margins entire; petioles to 2.5 cm long, 0.75 cm wide at the base, enlarging to 1.5 mm wide at the tips, densely brown pilose, hairs spreading, to 6 mm long. *Inflorescence* with the bracts ovate elliptic, to 3 cm long and 1 mm wide, the bracts apically caudate, the cauda ca. 5 mm long, shallowly cordate at the base, densely brown pilose on both the surfaces, spreading and ascending, to 6 mm long. *Flowers* with the calyx annular, ca. 2 mm long; corolla not seen; fruit obovate, flattened, 2.3 cm long, 1.3 cm wide, 5 mm thick, apically rounded, surface puberulous.

This species occurs in rain forests of Colombia and Panama.

The Panamanian specimen seen has smaller leaves and bracts than those described by Leonard (1951) for this species, but closely resembles it in all other respects. Leonard did not observe the corolla for his species description, nor was one observed in this study.

BOCAS DEL TORO: Big Bight, Chiriquí Lagoon, *Wedel 2887* (MO, US).

3. **Mendoncia costaricana** Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 113. 1855. TYPE: Cerro de Aquacate, Costa Rica, *Oersted* (not seen).

Herbaceous *vines*, the stem subquadrangular, grooved, strigose to subglabrous. *Leaves* elliptic to elliptic ovate, to 10 cm long, 7 cm wide, apically

abruptly acuminate and sometimes falcate, the apiculate tip to ca. 2 mm long, basally rounded but slightly short-attenuate, pilose above and beneath, sparingly scabrous above with hairs arising from obscure stellate bases, sparingly puberulous beneath, the margins entire; petioles to 4 cm long, sparingly strigose. *Flowers* axillary, borne singly or in pairs; pedicels ca. 2 cm long, strigose; bracts obovate, to 15 mm long, 11 mm wide, apiculate, basally subcordate, strigose outside, glabrous within; corollas white with dark spots at the throat, to 3 cm long, 8 mm wide at the throat, the lobes emarginate, 4–5 mm long, 4–5 mm wide; ovary glabrous. *Fruit* flattened ovoid with double margins, ca. 2 cm long, 1.3 cm wide, 4 mm thick, puberulous.

This species is found in wet forests of Costa Rica and Panama. The descriptions of bracts and corolla are from Leonard (1951) since these are not present on the specimen examined.

CHIRIQUÍ: Salta-Camisete trail, Volcán de Chiriquí, 5000 ft, *Terry 1361* (MO, US).

4. **Mendoncia gracilis** Turrill, Kew Bull. 418. 1919. TYPE: Mesa Grande on Río Negro, Department of Cundinamarca, Colombia, *Lehmann 8792* (Kew, not seen).

Suffrutescent *vine*, young stems strigose to sericeous and quadrangular. *Leaves* elliptic to elliptic ovate, to 12 cm long and 7 cm wide, apically acuminate, often with a mucro to 2 mm long, basally rounded to acute, the veins prominent, usually 4 pairs, strigose beneath and above, hairs above arising from stellate bases, the margins entire; petiole to 2 cm long, mostly 1.5 cm long, strigose to sericeous. *Inflorescence* axillary, the pedicels borne singly or in pairs, 1.5–2.0 cm long, strigose to sericeous; bracts ovate, entire, to 18 mm long and 13 mm wide, apiculate, basally rounded, glabrous inside, strigose to sericeous outside. *Flowers* with the calyx reduced to an entire membranous cup ca. 1 mm deep, glabrous; corolla white, funnelform, to ca. 3 cm long, basally 3 mm wide, 6 mm wide at the throat, the throat lined with reddish brown, oblique, the lobes 5–6 mm long, 4–5 mm wide, emarginate, the tube glandular puberulous inside below the stamens, glabrous outside, the throat glandular puberulous just above the stamens, the remainder of corolla glabrous. *Fruits* (immature) ovoid.

This species occurs along trails and openings in rain forests in Panama and Colombia.

CANAL ZONE: Pipeline Road 3 mi from Gamboa gate, *Croat 15097* (MO). Barro Colorado Island, *Croat 16519, 16530* (both MO); *Ebinger 645* (MO). PANAMÁ: El Jefe, *Duke 9443* (MO).

5. **Mendoncia hirsuta** (Poepp. & Endlich.) Nees in DC., Prodr. 11: 52. 1847.

Mendozia hirsuta Poepp. & Endlich., Nov. Gen. Sp. Pl. 3: 10. 1845. TYPE: between Maynas and Yurimaguas, Peru, *Poeppig 2252* (B, not seen).

Suffrutescent *vine*, young stems subquadrangular, grooved, tawny, pilose, the hairs 3–4 mm long. *Leaves* elliptic to elliptic obovate, to 11 cm long and 5 cm wide, acuminate with an apiculate tip ca. 5 mm long, basally acute, the pilose

hairs above and below ca. 3 mm long, the margins entire, the petioles ca. 1 cm long with tawny pilose hairs to ca. 3 mm long. *Inflorescences* axillary, the pedicels in pairs or single, pilose, to 2.5 cm long; bracts ovate, to 1.8 cm long, 1.2 cm wide, apically apiculate, basally rounded, densely pilose outside, glabrous inside. *Flowers* with the calyx glabrous; mature corolla not seen. *Fruit* not seen.

This species occurs in rain forests of Darién in Panama as well as Colombia, the Guianas, Peru and Bolivia. Duke (*13001*) reported that the Cuna of Darién use the fruits of this species to make necklaces.

DARIÉN: Forest, 1–4 mi N of Pucro, *Duke 13001* (MO).

6. **Mendoncia lindavii** Rusby, Mem. Torrey Bot. Club 4: 241. 1895. SYNTYPES: Yungas, Bolivia, *Bang* 532, *11707* (both US).

Suffrutescent *vines* climbing over trees and shrubs; stems densely villous with hairs to 4 mm in length and appressed. *Leaves* with elliptic blades 6–11.5 cm long, 2.5–6 cm wide, chartaceous, apically acuminate, basally rounded to obtuse, the upper surface with pilose hairs arising from stellate bases, the lower surface with ascending villous hairs, the petioles to 2.5 cm long. *Inflorescences* axillary, the pedicels borne singly or in pairs, to 3 cm long; mature bracts oblong lanceolate, to 4 cm long and 1 cm wide, apically attenuate and basally rounded; corolla red, pink or white, funnelform, to 5 cm long, 8 mm wide at the mouth, 6 mm at the base, glabrous, the 5 equal lobes to 6 mm long, 4.5 mm wide, apically retuse to rounded; stamens attached at about the midpoint of the corolla tube, the anthers to 1.5 cm long; ovary velutinous, ca. 4 mm long, 2.5 mm wide, style to 5 cm long, stigma forked. *Fruit* a flattened drupe, obovate, to 2 cm long, about 1 cm wide, oblique at the apex and terminated by a portion of the persistent style, dark brown and densely puberulent.

Usually found in damp areas in forests and thickets near streams or ponds, this species ranges from British Honduras and Guatemala as far south as Bolivia.

CANAL ZONE: Barro Colorado Island, *Croat 16530* (DUKE); *Foster 2359* (DUKE). COCLÉ: El Valle, 800–1000 m, *Duke 13205* (MO). DARIÉN: On hills above W end of airstrip at Caná near Río Cana, 500–550 m, *Croat 38065* (MO). Caná, 1750 ft, *Stern et al. 487, 673* (both MO). Caná, *Williams 789* (NY).

7. **Mendoncia litoralis** Leonard, Contr. U.S. Natl. Herb. 31: I. 1951. TYPE: Dept. of El Valle, Colombia, *Cuatrecasas 17529* (US).

Suffrutescent *vine*, young stems quadrangular, densely strigose, hairs 1–2 mm long. *Leaves* elliptic to 12 cm long, 6.5 cm wide, apically acuminate often with apiculate tip ca. 1 mm long, basally acute, sparingly strigose to near glabrous above, hairs mostly along the costa, the hairs with obscure stellate bases, more sparingly strigose beneath with most hairs restricted to the costa, the margins entire; petioles to 2 cm long, densely strigose. *Inflorescences* axillary, the pedicels borne singly or in pairs, to 2 cm long, densely pilose, the hairs to 2 mm long; bracts elliptic, to 1.8 cm long and 1 cm wide, apiculate, basally acute to rounded, the pilose hairs outside not appressed, to 2 mm long, glabrous inside;

calyx entire, glabrous, ca. 1 mm long; corolla purple, oblique to 3 cm long, tube 1.5 cm long, 4 mm wide at base, 7 mm wide at the throat, glabrous outside, puberulous glandular inside at the base of the stamens and at the throat just above the stamens, lobes ca. 5 mm wide and 4.5 mm broad, emarginate, glabrous; the anthers and the upper portion of filaments glandular puberulous; style 1.6 cm long, glabrous. *Fruits* ovoid, 1.5 cm long, ca. 1 cm wide, glabrous.

This species is found in mature rain forest along trails and roads of Colombia and adjacent Panama.

CANAL ZONE: Drowned forest near Vigia and San Juan on Río Pequeni, 66 m, *Dodge et al. 16680* (US). Road K-19, 2 mi from W border of Zone to cleared area near canal, *Gentry 1790* (NY). Pipeline road near Río Agua Salud, *Kennedy & Redemsky-Young 1840* (MO). BARRO COLORADO ISLAND: *Croat 4339, 4375, 8615, 11676, 12413, 12496, 12572* (all MO); *Ebinger 206* (MO), *645* (F); *Foster 1454* (MO); *Shattuck 83* (MO), *651* (MO, US). CHIRIQUÍ: Burica Peninsula, primary forest 10–11 mi W of Puerto Armuelles near San Bartolo Limite, 300–500 m, *Croat 21984* (MO). DARIÉN: Pinogana, ca. 20 m, *Allen 933* (MO). Trail from Paya to Payita, *Stern et al. 392* (MO). LOS SANTOS: Loma Prieta, Cerro Grande, 2400–2800 ft, *Lewis et al. 2227* (MO). PANAMÁ: Bald savannahlike areas along road toward top of Cerro Campana, *Duke 5991* (MO). Dam site near Río Bayano beyond Cañita, *Gentry & Tyson 1673* (MO). Juan Diaz, *Standley 30593* (MO, US). SAN BLAS: Mouth of Ailigandi River to 2.5 mi inland, often by native plantations, *Lewis et al. 169* (MO). Road from El Llano to Carti-Tupile, 300–500 m, *Liesner 1259* (MO).

8. **Mendoncia retusa** Turrill, Kew Bull. 423. 1919. TYPE: Manmee Station, Sect. 30, Panama, *Hayes 169* (not seen).—FIG. 21.

Suffrutescent *vines* with quadrangular stems narrowly winged; young stems and petiole sparsely strigose to glabrous in the older stems, the hairs to 0.5 mm long. *Leaves* elliptic, the blades 6–15 cm long, 2.5–7.5 cm wide, chartaceous, apically attenuate to acuminate, basally rounded to obtuse, ciliate, the upper surface sparsely strigose, the lower surface sparsely strigose at veins only, the petioles to 4.5 cm long. *Inflorescence* axillary, the pedicels one per axil, 1.75–3.0 cm long, the bracts green, oblong lanceolate, mostly glabrous, 1.5–3.0 cm long, 1.0–1.75 cm wide, mucronate at the tips and rounded bases. *Flowers* with the corolla white with purplish throat, 4–5 cm long, glabrous, 5-lobed, lobes 5–6 mm long, obtuse. *Fruit* irregularly obovate, 1.5 cm long, puberulent.

Mendoncia retusa is found in moist forests at lower elevations in Costa Rica and Panama.

BOCAS DEL TORO: Chiriquí Lagoon, *Wedel 359, 705, 845, 1088, 1140, 1551* (all MO). CANAL ZONE: Pipeline Road, *Mori & Kallunki 2405* (MO). BARRO COLORADO ISLAND: *Croat 8615* (DUKE); *Foster 835, 1234, 1370, 1454* (all DUKE). DARIÉN: El Río Yapé, *Bristan 1416* (MO); Rio Paya, trail from Paya to Payita, *Stern et al. 392* (MO). PANAMÁ: Bald savannahlike areas along road toward top of Cerro Campana, *Duke 5991* (MO).

9. **Mendoncia tonduzii** Turrill, Kew Bull. 413. 1919. TYPE: Tucurrique, Costa Rica, *Tonduz 12946* (US).

Suffrutescent *vine*, quadrangular, tawny, dense, pilose, the hairs 12 mm long mostly at the angles on the young stem, older stem with corky ridges to a width of 2 cm. *Leaves* elliptic to elliptic ovate, to 13 mm long, 8.3 mm wide, apically acuminate, often with an apicule to 2 mm long, basally acute to rounded, the

FIGURE 21. *Mendoncia retusa* Turrill.—A. Habit (×½).—B. Corolla (×½).—C. Stamen (×1½).—D. Pistil (×½). [After *Stern et al.* 392 (MO).]

pilose hairs with stellate bases above, more densely pilose beneath, 4–5 pairs of veins especially prominent beneath, the margins entire; petioles ca. 2 cm long with tawny, densely pilose hairs ca. 1.5 mm long. *Inflorescences* axillary, the pedicels borne singly or in pairs, to 2.5 cm long, densely pilose; bracts oblong to oblong ovate, to 4 cm long, 1.5 cm wide, rounded apically and basally with a short mucro 0.5 mm long, covered with pilose hairs, densely tawny pilose outside, glabrous inside. *Flowers* with the corolla white, ca. 5 mm long, 8 mm wide at the oblique throat, the lobes emarginate, spreading ca. 8 mm long, 5–6 mm wide, glabrous. *Fruit* ovoid purplish black at maturity, ca. 1.8 cm long, 1.1 cm wide, 0.5 cm thick, densely puberulous.

Leonard reports this species as rare except at the type locality. More recent collections have extended the range although it is not found common in its lowland rain forest habitat. Corolla measurements were taken from Leonard's (1937–38) description. One collector reports Costa Rican flowering as nocturnal.

COCLÉ: El Valle, 800–1000 m, *Duke 13205* (MO). COLÓN: Santa Rita Ridge E of Transisthmian Highway, 300–500 m, *Gentry 6097* (MO).

22. NELSONIA

Nelsonia R. Br., Prodr. 480. 1810. TYPE: *Justicia brunelloides* Lam.

Herbs, softly villous. *Leaves* entire. *Inflorescences* dense, terminal and axillary spikes with a single bract. *Flowers* with the calyx 4-lobed; corolla blue or purple, bilabiate; stamens 2, the anthers 2-celled, the cells parallel, each cell globose; stigma 2-lobed. *Capsules* oblong; seeds borne on papilliform funicles.

There is only one species described for this genus which was first collected in Java. The genus is named for David Nelson, a gardener who accompanied Cook on his last voyage.

1. **Nelsonia brunelloides** (Lam.) Kuntze, Rev. Gen. Pl. 2: 493. 1891.—FIG. 22.

Justicia brunelloides Lam., *tab. 1.* Encycl. Méth. 1: 40. 1791. TYPE: Java (not seen).
Nelsonia albicans H.B.K., Nov. Gen. Sp. Pl. 2: 234. 1817. TYPE: Colombia (not seen).

Herbs, decumbent to ascending with narrow, branching stems to 40 cm long. *Leaves* opposite, ovate, 1–8 cm long, 0.5–3.0 cm wide, acute to obtuse at the apex, villous above and beneath, the margins undulate. *Inflorescences* dense spikes to 2.5 cm, pedunculate or sessile, mostly axillary, the flowers sessile, or with pedicel ca. 1 mm long or obsolete; bract single, 4–6 mm long, ovate, acuminate, velutinous, imbricate. *Flowers* with the sepals 4, upper and lower acute, ca. 4 mm long; corolla deep purple to blue, the tube ca. 3 mm long, the limb 2-lipped, the upper lip 2-cleft, the lower lip 3-lobed, ca. 5 mm long. *Capsule* sessile, ca. 5 mm long, ca. 10 seeds per locule.

According to Leonard (1958) this species is partial to moist sandy places. It ranges from Mexico, Central America, and the West Indies to northern South America and the Old World Tropics.

FIGURE 22. *Nelsonia brunellioides* (Lam.) Kuntze. Habit (×9/10). [After *Dwyer et al. 4148* (MO).]

CANAL ZONE: Barro Colorado Island, *Croat 8051*, *8221* (both MO). Pipeline Road, T.T.C. transect 3, along railroad tracks, *Gentry* 7399 (MO). COCLÉ: Boca del Toabré at confluence of Río Toabré and Río Coclé del Norte in pasture, *Lewis et al. 5486* (MO). PANAMÁ: Hills above Campana 600–800 m, *Allen 1696* (MO). Goofy Lake, *Dwyer et al.* 4148 (MO).

23. NERIACANTHUS

Neriacanthus Benth. in Benth. & Hook. Gen. Pl. 2: 1096. 1876. TYPE: *N. purdicanus* Benth.

Aphanandrium Lindau in Engl. & Prantl, Nat. Pflanzenfam. IV, 3b: 323. 1895. TYPE: *A. lehmannianum*.

Shrubs. *Leaves* opposite with entire or undulate margins. *Inflorescences* of terminal or axillary spikes; bracts imbricate, usually colored, conspicuous; bractlets about the same size as the deeply 5-parted calyx segments; corolla tube subcylindric, the lobes imbricate, subequal, spreading; stamens 4, included, the anthers narrow, 1-celled. *Capsules* short stipitate, minutely punctate, shiny, glabrous, 4-seeded; seeds flattened, suborbicular, borne on blunt-tipped retinacula.

Three species have been described for this genus which is endemic to tropical America. They range from Peru to Panama.

1. **Neriacanthus grandiflorus** Leonard, Contr. U.S. Natl. Herb. 31: 121. 1953. TYPE: Colombia, *Cuatrecasas 15625* (US, not seen).—FIG. 23.

Shrubs 1–2 m tall; stems subquadrangular, sometimes swollen at the nodes in young portions, glabrous. *Leaves* elliptic to elliptic obovate, 10–21 cm long, 2.5–7 cm wide, apically acuminate, basally attenuate, drying dark green above, lighter green below, cystoliths present but obscure, glabrous, gland dotted below, the margins entire to undulate; petioles 1–2.5 cm long, glabrous. *Inflorescences* in terminal spikes to 9 cm long, 1.5–3 cm wide, borne singly and in pairs; peduncles to 7 cm long, glabrous; rachis glabrous to puberulous; bracts white to green or purplish, imbricate, elliptic to elliptic oblong, to 2.5 cm long, 1.25 cm wide, apically acute, 10–12 veined, glabrous, minutely gland dotted, the margins serrulate toward the tip with teeth ca. 0.25 mm long; bracteoles narrowly lanceolate, to 7.5 mm long, 1 mm wide at the base, glabrous. *Flowers* with the calyx segments lanceolate, apically acuminate, glabrous, the posterior segment to 4.25 mm long, 1.5 mm wide, lateral segments to 4 mm long, 0.75 mm wide, anterior segments to 4 mm long, 1.0 mm wide; corolla with white tube and lavender lobes, the tube cylindrical, 3–3.8 cm long, 5–9 mm wide, apically obtuse to rounded; stamens inserted ca. 2 cm above the base of the tube, filaments 1 mm long, pilosulous; anthers 2.5 mm long, 0.5 mm broad, apically adherent. *Capsules* clavate, 11 mm long, 4.5 mm broad, 3 mm thick, minutely punctate, glabrous; seeds ovate, 4 mm long, 3 mm broad, dark brown when dry.

This species is found in cloud forest areas at elevations of 700–1,500 m in Colombia and Panama.

CHIRIQUÍ: Cerro Colorado, 50 km N of San Félix on the continental divide in cloud forest, 1200–1500 m, *Mori & Dressler 7787* (MO). VERAGUAS: Between Escuela Agrícola and Alto

FIGURE 23. *Neriacanthus grandiflorus* Leonard. Habit (×⅝). [After *Mori & Kallunki 6196* (MO).]

Piedra on Río dos Bocas 5–8 km from Escuela, 730–770 m, *Croat 25919* (MO). NW of Santa Fe 2 km from Escuela Agrícola Alto de Piedra, cloud forest on ridge below summit of Cerro Tute, *Mori & Kallunki 5293* (MO). NW of Santa Fe 8.8 km from Escuela Agrícola Alto de Piedra, Pacific slope, hillside above stream, *Mori & Kallunki 6196* (MO). Trail up E side of Cerro Tute, 1200 m, *Witherspoon et al.* 8869 (MO).

24. ODONTONEMA

Odontonema Nees, Linnaea 16: 300. 1842. TYPE: *O. lucidum* Nees.

Thyrsacanthus Nees in Mart., Fl. Bras. 9: 97, *pl. 13*. 1847. TYPE: *T. barlerioides* Nees.

Herbs or *shrubs*. *Leaves* often large with the cystoliths visible on both the surfaces, sessile to petiolate. *Inflorescences* in terminal panicles or thyrses with inconspicuous bracts. *Flowers* white, red or yellow, 5-merous; calyx with equal, subulate segments; corolla bilabiate, the upper lip 2-lobed, the lower 3-lobed; stamens 2, exserted or extending to the mouth, the anthers 2-celled with the

cells parallel and blunt at the base, staminodes 2. *Capsules* clavate, bearing 4 seeds.

This genus has about 40 species and is found only in the New World Tropics.

a. Leaves under 10 cm long; inflorescences in racemes with most flowers borne singly ---------- 4. *O. microphyllus*
aa. Leaves to over 15 cm long; inflorescences thyrsoid or in racemes with the flowers in fascicles.
  b. Leaves under 5 cm wide; corolla to 2.5 cm long ---------- 3. *O. longifolium*
  bb. Leaves over 8 cm wide; corolla over 2.5 cm long.
    c. Inflorescences terminating in a narrow, flowerless tip; corolla to 2.8 cm long ---------- 2. *O. flagellum*
    cc. Inflorescences flowering to the tip; corolla to 3.0 cm or more long.
      d. Inflorescences with the lateral axes in dichasia; corolla to 3.0 cm long ---------- 1. *O. callistachyum*
      dd. Inflorescences with the flowers in pseudowhorls, not lateral dichasia; corolla over 3 cm long ---------- 5. *O. strictum*

1. **Odontonema callistachyum** (Schlecht. & Cham.) Kuntze, Rev. Gen. Pl. 2: 494. 1891.

Justicia callistachya Schlecht. & Cham., Linnaea 6: 370. 1831. TYPE: Mexico, *Schiede* (B?, not seen).

Thyrsacanthus callistachyus (Schlecht. & Cham.) Nees in DC., Prodr. 11: 326. 1847.

Suffrutescent *herb* to 2 m tall; stems subquadrangular, glabrous to puberulous. *Leaves* elliptic to elliptic ovate, 15–30 cm long and 4–12 cm wide, apically acuminate with the tip often curved to one side, basally attenuate, glabrous above, puberulous beneath along the midrib and the major costa, the cystoliths visible on both surfaces, more so above, the margins entire to crenulate; petioles wanting or to 1 cm long. *Inflorescences* in terminal thyrses to 30 cm long, the lateral peduncles to ca. 5 mm long, the flowers in fascicles, each fascicle subtended by a subulate, keeled, puberulous bract 2–3 mm long, the flowers mostly borne in dichasial cymes, each subtended by a similar, though slightly smaller, more triangular bract; rachises subtomentose to tomentose; pedicels 3–6 mm long, puberulous to tomentose. *Flowers* with the calyx 5-merous, the segments equal, subulate, keeled, puberulous, 2–3 mm long; corolla red, bilabiate, funnelform, often curved to one side, to 3.0 cm long, 5 mm wide at the throat and 2 mm wide at the base, the tube puberulous on both surfaces, the upper lip 6–7 mm long, 4.5 mm wide at the base, 2-lobed, the lobes ovate, 4.5 mm long, 2.5 mm wide, apically obtuse, the lower lip of 3 lobes, each 7–8 mm long, 2 mm wide, apically obtuse; stamens extending to or just beyond the notch of the upper lip, the filaments villous, the staminodes to 3.5 mm long, the apex slightly enlarged, curved and apiculate, the sterile anthers puberulous, the filaments glabrous. *Capsule* not observed.

This species is found in rain forests at lower elevations of Mexico and Central America.

COCLÉ: La Mesa, above El Valle, *Dwyer 11902* (MO). Ca. 8 mi N of El Valle de Antón, *Luteyn & Kennedy 1694* (DUKE). COLÓN: Río Guanche, *D'Arcy 9718* (MO). DARIÉN:

Camp Summit between Morti and Sasardi, 1800 ft, *Child & Duke 10690* (MO). Near Cerro Pirre base camp on Río Perasenico, 200–500 m, *Gentry & Clewell 7053* (MO). Manene to mouth of Río Cuasi, *Kirkbride & Bristan 1388* (MO). Between Tres Bocas and Cerro Campamiento on Cuasi-Cana Trail, *Kirkbride & Duke 1346* (MO). PANAMÁ: Cerro Azul, near Goofy Lake, *Dwyer 2076B* (MO). Capira, NE side of Cerro Trinidad, 800 m, *Foster 2107* (DUKE). Cerro Campana, *Luteyn & Kennedy 1800* (DUKE). Cerro Azul, 2000 ft, *Tyson 2180* (MO). Cerro Campana, 2000 m, *Weaver & Foster 1680* (DUKE). SAN BLAS: Lower Río Ailigandí, *Duke 9321* (MO).

2. **Odontonema flagellum** (Oerst.) Kuntze, Rev. Gen. Pl. 2: 494. 1891.

Thyrsacanthus flagellum Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1854: 146. 1855. TYPE: Costa Rica, *Oersted* (C, not seen).

Shrub to 2.5 m; stem quadrangular, sparingly puberulous in young portions. *Leaves* elliptic to 34 cm long, 10.5 cm wide, apically acuminate, basally attenuate, glabrous to slightly puberulous at the costa above, puberulous at the costa and the veins beneath, the cystoliths numerous, more visible above than beneath, the margins crenulate to nearly entire; petioles short and winged, mostly 0.5 cm or less, puberulous to glabrate. *Inflorescences* racemose to 50 cm long, flowers in fascicles of 2 or 3 toward the bottom, single toward top, the top ending in a narrowed, flagellate tip; bracts subulate, keeled to 5.5 mm long, 1.5 mm wide at base, apically acuminate, 3-nerved, puberulous, ciliolate; bracteoles subulate, keeled, to 4 mm long, 1 mm wide at base, puberulous; rachis quadrangular, puberulous to glabrate; peduncle quadrangular, to 6 cm long, puberulous. *Flowers* with the calyx reddish margined when dry, the 5 equal, subulate segments to 3.5 mm long, 1 mm wide at the base, sparingly puberulous; corolla dark to brilliant red to 2.8 cm long, funnelform and curved to one side, 6 mm wide at the mouth, 2 mm wide at the base, the tube glabrous on both the surfaces, bilabiate, the upper lip 5 mm long, 4 mm wide at base, 2-lobed, lobes 2 mm long, apically obtuse and ciliolate, the lower lip 3-lobed, the lobes slightly shorter than those of the upper lip, 3 mm wide at the base, apically obtuse and ciliolate, all lobes with glandular hairs inside; stamens reaching the corolla mouth or slightly exserted, the staminodes ca. 6 mm long, curved and pointed at the apex. *Capsules* clavate, 1.8 cm long, 4 mm wide at the widest point, 1.2 mm wide at the base, glabrous; seeds elliptic, 5 mm long, 3 mm wide, flattened, 1 mm thick, surface reddish brown when dry, muricate.

This species is found in forests of Costa Rica and western Panama.

BOCAS DEL TORO: 10–15 mi inland S of mouth of Changuinola River, *Lewis et al. 882* (MO). Chiriquicito to 5 mi S along Río Guarumo, *Lewis et al. 2034* (MO). Almirante near road to Chiriquí, *McDaniel 5054* (MO). Almirante Bay, Western River, *Wedel 21* (MO). Chiriquí Lagoon, *Wedel 1009, 1318, 2023, 2327, 2774* (all MO). CHIRIQUÍ: Woods above Alto Lino, 4000–4500 ft, *Maurice 843* (US). COLÓN: Río Guanche, 1–4 km upstream from Portobelo Road, tropical wet forest, 0–100 m, *Gentry 8763* (MO). PANAMÁ: Along trail to top of Cerro Campana, *Mori & Kallunki 2481* (MO).

3. **Odontonema longifolium** (Oerst.) Kuntze, Rev. Gen. Pl. 2: 494. 1891.

Thyrsacanthus longifolius Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1854: 145. 1854. TYPE: Nicaragua, *Oersted* (C, not seen).

Herb to 2 m tall; stem subquadrangular, puberulous. *Leaves* elliptic oblong, to 16 cm long and 3.5 cm wide, apically acuminate, basally attenuate, glabrous

above and beneath, the cystoliths visible on both the surfaces, the margins entire, the upper leaves sessile, entire or slightly undulate, the lower leaves with short petioles to ca. 4 mm long. *Inflorescences* in a terminal thyrse to 7 cm long, lateral axes in dichasia, the rachis and the pedicels puberulous; one bract subtending each flower and each peduncle, subulate, keeled, to ca. 5 mm long and 0.6 mm wide at the base, puberulous. *Flowers* with 5-lobed calyx, the lobes equal, subulate, to 2.5 mm long, 0.5 mm wide at base, puberulous; corolla bright red, bilabiate to ca. 25 mm long, 2.5 mm wide at the base, 6 mm wide at the mouth, puberulous outside and inside the tube, the upper lip ca. 11 mm long and 7.5 mm wide at the base, 2-lobed, the lobes 3 mm long, apically acute, the lower lip 11 mm long, 5 mm wide, 3-lobed, the lobes oblong, apically acute, both the lobes with small glandular hairs inside, puberulous outside; stamens exserted, the anthers puberulous, the filaments glabrous, the staminodes coalesced to the filaments of the fertile stamens and emerging from them about one third of the distance up the filament, the free portion of staminode ca. 1.5 mm long, sparingly ciliolate, slightly enlarged apically; ovary at anthesis ca. 3 mm long, beaked with a globose base, glabrous. *Capsules* not seen.

This species is found at edges of forest along streams and rivers.

CANAL ZONE: Along streams, drowned forest of Quebrada Ancha, 70 m, *Dodge & Steyermark 17043* (MO). 6–8 mi N of Gamboa, *Gentry 3357* (MO). COLÓN: Near Peluca, on Río Boquerón, ca. 27 km from Transisthmian Highway, *Dressler 4263* (MO). Alrededores de Salamanca, *Lezcano 41* (MO). DARIÉN: Summit Camp, between Sasardí and Mortí, ca. 400 m, *Duke 10032* (MO). Teotuma, Hansteina, ca. 100 m, *Duke 10072* (MO). Forest 1–3 mi N of Paya, *Duke & Kirkbride 14009* (MO). Río Aretí, *Duke & Nickerson 14908* (MO). Río Pirre, trail up river from house of Bartolo, *Kennedy 2879* (MO). 4.5 km S of El Real, *Mori & Kallunki 5417* (MO). PANAMÁ: Semiswampy floodplain near bridge over Río Buenaventura, near Portobelo, *Foster & Kennedy 1792* (DUKE). Tributary of Río Chagres, 5 mi SW of Cerro Brewster, ca. 1000 ft, *Lewis et al. 3437* (MO). Gorgas Memorial Labs yellow fever research camp, ca. 25 km NE of Cerro Azul on Río Piedras, 550 m, *Mori & Kallunki 3381, 3471* (both MO). Banks of Mamoní River above Chepo, 20–25 m, *Pittier 4726* (US). SAN BLAS: Sasardí, frequent along San Blas rivers, ca. 20 m, *Duke 10134* (US). VERAGUAS: On road from Santa Fé to Calovebora (Panamian Highway 35), 16 km from Santa Fé, on Atlantic slope near Río Caloveborita, *Mori et al. 6676* (MO).

4. **Odontonema microphyllus** Durkee.[12] TYPE: Panama, *Kennedy 2762* (MO). —FIG. 24.

Shrub to 1.5 m tall, often decumbent; stems subquadrangular in younger portions, glabrous to puberulous, appearing jointed at the internodes. *Leaves* elliptic to elliptic-ovate, 3–5 cm long and 1–1.7 cm wide, apically acuminate, basally attenuate, glabrous on both sides, the cystoliths minute, visible only on the upper surface, the margins entire to undulate; petioles short, 2–4 mm long, pubescence that of the stem. *Inflorescences* in loose, terminal racemes to 7 cm

[12] *Odontonema microphyllus* Durkee, sp. nov. Frutex ad 1.5 m altus, saepe decumbens; foliis ellipticis ad ovato-ellipticis, 3.5 cm longis, 1.0–1.7 cm latis, utrinque glabris, cystolithis minutis, tantum supra manifestis, marginibus integris vel undulatis; petioles brevis, 2–4 cm longis; inflorescentibus terminalibus, racemis laxis ad 7 cm longis constantibus, bracteis plerumque floribus solitariis, interdum geminis gerentibus; pedicellis 3–6 cm longis; corolla rubra vel miniata ad 2.3 cm longa, 6 cm lata; staminibus incisura labii supremi leviter superantibus.

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long, pedicels mostly one per bract with occasional pairs, each 1 or occasional pair subtended by a single subulate bract, ca. 1 mm long, 0.5 mm wide at the base; bracteoles, 2 per flower, immediately inside each bract and of similar shape and size; rachis glabrous to puberulous; pedicels 3–6 mm long, the pedicels puberulous. *Flowers* with the calyx segments subulate, 2–3 mm long, 0.5 mm wide at base, ciliolate; corolla red or red-orange, bilabiate, funnelform, often curved to one side, to 2.3 cm long, 6 mm wide at the throat and 2 mm wide at the base, puberulous outside, mostly glabrous inside except for a few short glandular hairs on the inner surface of the lobes, upper lip 5 mm long, 5 mm wide at the base, 2-lobed, the lobes ovate, 3 mm long, ca. 3 mm wide at the base, the lower lip 3-lobed, each lobe ovate, 5.5 mm long, 3 mm wide at base, apically obtuse; stamens extending to just beyond the notch of the upper lip, the anthers 2 mm long, the filaments glabrous, the staminodes 2.5–3 mm long, apically apiculate and curved to one side, glabrous. *Capsules* 4-seeded, clavate, 2 cm long, 4 mm broad, 4 mm thick, minutely puberulous; seeds oval, flattened, 3 mm long, 2.5 mm wide ca. 1 mm thick, the surface roughened.

This species grows in low forests and mountain slopes.

COLÓN: Santa Rita, abandoned lumber road N of Agua Clara rain gauge, *Kennedy 2762* (MO). PANAMÁ: Cerro Jefe, *Duke 8004, 9457* (both MO); *Dwyer 8368* (MO); *Gentry 2877* (MO). La Eneida, Cerro Jefe region, 750 m, *Maas & Dressler 694* (MO). E slope of Cerro Jefe, 2700 ft, *Tyson 3375* (MO). Edge of forest along the Cartí Road between about 10–12 km from its intersection with the Panamanian Highway beyond Chepo, *Wilbur & Luteyn 19528* (DUKE). Slopes of Cerro Jefe beyond Cerro Azul ca. 5.5 mi on road to La Eneida, 2700–3000 ft, *Wilbur & Teeri 13639* (DUKE). Slopes of Cerro Jefe beyond Cerro Azul between 4–8 mi in mostly heavily wooded slopes, *Wilbur & Weaver 11378* (DUKE). Forested slopes of Cerro Jefe, *Wilbur et al. 11323* (DUKE). Slopes of Cerro Jefe between Cerro Azul and La Eneida ca. 15 mi NE of Panama City, *Wilbur et al. 15543* (DUKE).

5. **Odontonema strictum** (Nees) Kuntze, Rev. Gen. Pl. 2: 494. 1891.

Thyrsacanthus strictus Nees in DC., Prodr. 11: 324. 1847. TYPE: Honduras, *Armstrong* (not seen).

Suffrutescent, to 2.5 m high; stems subquandrangular, glabrous to sparingly pilose. *Leaves* elliptic to oblong elliptic, to 32 cm long, 9 cm wide, apically acuminate with the tip often curved to one side, basally narrowed to a rounded base, 5–8 mm wide, both the surfaces glabrous, numerous, minute cystoliths visible on the upper epidermis, the lower leaves sessile, the upper leaves with short, glabrous petiole to 4 mm long. *Inflorescences* in terminal racemes to 14 cm long, the rachis glabrous to puberulous, quadrangular, the flower clusters to ca. 1.5 cm apart on the lower rachis, arranged in pseudowhorls; bracts subulate, length variable, 8–25 mm long, mostly 10 mm or less, 2 mm wide at the base, keeled, acuminate, the surface sparingly puberulous, ciliolate, one bract frequently subtending 2 or 3 flowers each bearing a smaller bract and with triangular bracteoles ca. 1.0 mm long, 1.0 mm wide at the base, sparingly puberulous,

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FIGURE 24. *Odontonema microphyllus* Durkee. Habit (×¾). [After *Kennedy 2762* (MO).]

acuminate; peduncle quadrangular, mostly glabrous, to 3.5 cm long; pedicels short, mostly glabrous, to 1 cm long, frequently borne in clusters of 3. *Flowers* with the calyx segments reddish when dry, equal, subulate, to 3.0 mm long, 1.0 mm wide at the base, acuminate, sparingly puberulous, sparingly ciliolate; corolla scarlet, bilabiate, funnelform, often curved to one side, to 3.5 cm long, 7 mm wide at the throat, 3 mm wide at the base, the tube glabrous on both surfaces, the upper lip 7.5 mm long, 6 mm wide at base, 2-lobed, the lobes ovate, 4.5 mm long, 3 mm wide, acuminate, ciliolate, glandular-hairy inside, the lower lip of 3 lobes, each ca. 7 mm long, 3 mm wide, oblong ovate, apically obtuse, ciliolate, the glandular hairs covering the inner surface of all the lobes; stamens extending to the notch of the upper lip, the staminodes 0.5–1 mm long, somewhat keeled and curved at the apex. *Capsules* clavate, to 2 cm long, 5 mm wide at the widest point, 2 mm wide at the base; seeds flattened, semiorbicular, 3 mm long, 2.5 mm wide, 1 mm thick, the surface heavily muricate.

This species is found in forests of Central America.

BOCAS DEL TORO: Forest above RR stop at Milla 7.5 at edge of creek, *Croat & Porter 16251* (MO). Río Teribé, mostly secondary growth near Quebrada Lukulon, ca. 300 ft, *Kirkbride & Duke 517* (MO). Nievecita, 0–50 m, *Woodson et al. 1812* (MO). CANAL ZONE: Forest along small unnamed quebrada entering lake at 70 m level, Río Indio, *Dodge & Allen 17303* (MO). Forest along banks of Quebrada La Palma and canyon of Río Chagres, 70–80 m, *Dodge & Allen 17382* (MO). CHIRIQUÍ: Woods around and above Alto Lino, 4000–4500 ft, *Maurice 843* (US). San Bartolo Limité, 20 km W of Puerto Armuelles, 400–600 m, in forest, *Busey 540* (MO). Bajo Mono, Boquete District, 4500 ft, *David 490* (MO). COCLÉ: El Valle de Antón, along Río Indio trail, 500–700 m, along streams, *Allen & Hunter 312* (MO). El Valle, 600–1000 m, *Allen 1226* (MO). North rim of El Valle de Antón, 600–1000 m, *Allen 1670* (F). Road to El Cope from Interamerican Highway, *Burch et al. 1381* (MO). Cloud forest near La Mesa, *Croat 13356* (MO). La Mesa, *Dwyer & Duke 8266* (MO); *Gentry 6829* (MO); *Kennedy et al. 3023* (MO); *Lewis et al. 2611* (MO). 2 mi N of Cerro Pilón, ca. 900 m, *Liesner 715* (MO). Foot of Cerro Pilón above El Valle de Antón, 2000 ft, rain forest, *Porter et al. 4410* (MO). Above Penonomé, Bismark, 2000–3000 ft, *Williams 590* (NY). DARIÉN: Between Upper Río Membrillo and Camp 7 on the construction road to San Blas 100–800 m, *Duke 10915* (MO). Caná, *Williams 746* (NY). PANAMÁ: Cerro Campana along trail to summit, *Croat 17168* (MO). Cerro Campana, lower slopes above FSU cabin, 850 m, *Croat 22771* (MO). Forests along headwaters of Río Corso off Río Pacora, 500 m, *Duke 11910* (MO). On trail to Cerro Campana, *Kirkbride & Hayden 278* (MO). Cerro Campana, *Lewis et al. 3042* (MO). Tributary of Río Chagres, 5 mi SW of Cerro Brewster, ca. 1000 ft, sandy and rocky river banks, *Lewis et al. 3440* (MO). La Eneida, Cerro Jefe region, 750 m, *Maas & Dressler 683* (MO). Cerro Campana, above Su Lin Motel, rain forest, *Porter et al. 4279* (MO). Cerro Campana, low cloud forest near the summit, *Smith & Smith 3368* (F). VERAGUAS: Santa Fé, forested slopes of Cerro Tute, 2500 ft, *Allen 4401* (MO). Primary forest on Caribbean slope above Río Primero Brazo 5 mi NW of Santa Fé, 700–1200 m, *Croat 23117* (MO). 3–5 mi N of Santa Fé, 500–1000 m, *Gentry 2958* (MO). Primary forest, 700–1200 m on Caribbean slope above Río Primero Brazo 5 mi NW of Santa Fé, *Liesner 833* (MO). PROVINCE UNKNOWN: *Duke 6160* (MO).

25. PSEUDERANTHEMUM

Pseuderanthemum Radlk., Sitzungsber. Math.-Phys. Kl. Bayer. Akad. Wiss., München 13: 282. 1883. TYPE: *E. alatum* Nees.

Herbs or small *shrubs*. Leaves ovate or elliptic. *Inflorescences* in terminal or axillary spikes, racemes or panicles; 1 bract and 2 bracteoles subtending

each flower or flower cluster. *Flowers* with the calyx segments 4 or 5, subulate; corolla white, blue, purplish or pink, the tube narrow, the limb spreading, the 5 lobes subequal; stamens 2, included or exserted, the staminodes 2, minute, the anther cells basally obtuse or acute. *Capsules* long stipitate; seeds 2 or 4.

This genus has 120 species from Old and New World Tropics.

a. Leaves basally cordate or subcordate; inflorescences racemose ..... 2. *P. cordatum*
aa. Leaves basally rounded and/or attenuate; inflorescences in panicles or spikes.
  b. Inflorescences in spikes; rachis of inflorescence puberulous or glandular puberulous.
    c. Calyx glabrous; flowers clustered in pseudowhorls on the rachis ..... 3. *P. cuspidatum*
    cc. Calyx glandular puberulous; flowers borne singly and alternating on the rachis ..... 4. *P. standleyi*
  bb. Inflorescences in panicles; rachis of inflorescence glabrous ..... 1. *P. atropurpureum*

1. **Pseuderanthemum atropurpureum** (Bull) Bailey, Gentes Herb. 1: 130. 1923.

Eranthemum atropurpureum Bull. Gard. Chron. 1: 619. 1875. TYPE: Cultivated in England, Bull (not seen).

Shrubs or small *trees* to 4 m high; stems subquandrangular toward the apex, glabrous except for a tuft of hair at or near the stipular ring. *Leaves* elliptic ovate, to 10 cm long and 6 cm wide, apically acute to apiculate, basally attenuate, the cystoliths nearly punctiform, greenish beneath and dark purple above, glabrous, the margins entire; petioles ca. 1.5 cm long, glabrous. *Inflorescences* terminal and axillary, in thyrsoid panicles with the flowers in subsessile fascicles of mostly 3 flowers; pedicels, peduncles and rachis glabrous, the pedicels to 5 mm long, the peduncles to 7 mm long and the rachis to 13 cm long, the lower bracts spatulate, ca. 7 mm long and 3 mm wide, the upper bracts progressively smaller and linear, all the bracts ciliolate. *Flowers* with 5-merous calyx, the lobes subulate, to 3 mm long, 1 mm wide at the base, ciliolate; corolla white with magenta spots in the throat, the tube cylindrical, to 10 mm long, 2.5 mm wide, the limb to 20 mm broad, the lobes elliptic, to 8 mm long, 5 mm wide, apically rounded, the margins ciliolate; stamens exserted, attached just below the mouth of the corolla, the filaments glabrous, the staminodes ca. 0.5 mm long, the anther cells acute at the base; ovary glabrous. *Capsules* not observed.

This species is frequently cultivated in tropical America and sometimes escapes. It is probably native in Polynesia.

CANAL ZONE: Hospital grounds at Ancón, 20–80 m, cultivated, *Pittier 3961* (US). Mount Hope Cemetery, *Standley 28845* (US). COLÓN: Guaira, mainland opposite Isla Grande, *D'Arcy 4047* (MO). PANAMÁ: Piria, ca. 150 m, *Duke 14443* (MO).

2. **Pseuderanthemum cordatum** (Nees) Radlk., Sitzungsber. Math.-Phys. Kl. Bayer. Akad. Wiss., München 13: 286. 1883.—FIG. 25.

Eranthemum cordatum Nees in Benth., Bot. Voy. Sulphur 147. 1844. TYPE: Chile (not seen).

Herbs to small shrub 1 m tall; stems erect, terete. *Leaves* ovate, to 20 cm long, 12 cm wide, apically acuminate, basally subcordate, glabrous, cystoliths

FIGURE 25. *Pseuderanthemum cordatum* (Nees) Radlk.—A. Habit (×3/5).—B. Inflorescence (×1).—C. Capsule (×1⅘). [After *Kennedy 2655* (MO).]

moderately distributed, visible on both the surfaces, the margins undulate to crenulate; petioles to 9 cm long, glabrous. *Inflorescences* in terminal racemes to 50 cm long, 2 cm wide; rachis terete, puberulous; bracts triangular to subulate, to 2 mm long, 1 mm wide basally, puberulous; pedicels borne in clusters of up to 6 at the base of the inflorescence to 1 at the top, 1–2 mm long, puberulous, the clusters to 3 cm apart at the base of the inflorescence. *Flowers* with the calyx 5-merous, the segments linear, 10–25 mm long, 0.5 mm wide, mi-

nutely puberulous glandular; corolla light to dark purple, puberulous, the tube cylindrical, 1.5–4 cm long, ca. 1.25 mm in diameter expanding to 3 mm around the ovary, the lobes of the limb oval, to 9 mm long, 4 mm wide; stamens exserted to ca. 6 mm beyond the mouth, the staminodes minute, barely discernible. *Capsules* to 16 mm long, 5 mm wide, 2 mm thick, puberulous; seeds 2, orbicular, flattened, 4 mm in diameter, roughened.

This species is found along stream banks and other shady moist habitats at lower elevations in central Panama.

CANAL ZONE: Drowned forest of Quebrada Ancha, 70 m, *Steyermark & Allen 17103* (MO). COLÓN: Disturbed forest of steep hill behind Portobelo, *Croat & Porter 15604* (MO). Río Guanche, *D'Arcy 9695* (MO). Near Peluca, km 25.6 from Transisthmian Hwy. on the road to Nombre de Dios, upstream on tributary to Río Boqueron, *Kennedy 2655* (MO). PROVINCE UNKNOWN: Boca de Cupé, *Williams* 684 (NY).

3. **Pseuderanthemum cuspidatum** (Nees) Radlk., Sitzungsber. Math.-Phys. Kl. Bayer. Akad. Wiss., München 13: 286. 1883.

Eranthemum cuspidatum Nees in Benth., Pl. Hartw. 148. 1839. TYPE: Mexico, *Hartweg* (K, not seen).

Herbs to 40 cm tall; stems erect, subquadrangular, glabrous to puberulous, the hairs restricted to 2 lines in some. *Leaves* ovate, 4–20 cm long, 2–10 cm wide, apically acuminate, basally rounded and then long attenuate, glabrous to sparingly strigose above, puberulous beneath, mostly on the costa and the veins, the cystoliths dense, more prominent above, the margins entire to crenulate; sessile or with unwinged petioles to ca. 5 mm long, pubescent as on the stem. *Inflorescences* in lax, terminal spikes to 14 cm long, the rachis puberulous; bracts subulate, to 3 mm long, 1.25 mm wide basally, ciliolate; bracteoles similar though smaller; lowermost pair of bracts suborbicular, to 2 cm long, 1.5 cm wide; flowers sessile, solitary or in clusters of up to 5 in pseudowhorls of up to 1 cm apart on the rachis. *Flowers* with the calyx 5-merous, the segments subulate, to 3 mm long, 0.5 mm wide, glabrous; corolla purplish, glabrous, tube cylindrical, to 4 cm long, 1 mm in diameter, lobes of the limb elliptic, ca. 8 mm long, 5 mm broad; stamens barely exserted, the filaments 2.5 mm long, staminodes 0.5 mm long. *Capsules* 12–16 mm long, 3 mm wide, 1.5 mm thick; seeds 4, orbicular, flattened, 2 mm diameter, roughened.

This species grows along stream banks and adjacent to forests at lower elevations in southern Mexico, Central America and northern South America.

CANAL ZONE. Madden Dam, second growth, *Ebinger 881* (MO, US). DARIÉN: Caná, 2000 ft, *Williams 784* (NY). PANAMÁ: Upper Tapia River, *Cornman 2032* (US). Alhajuela, Chagres River, *Killip 3215* (US). Alhajuela, *Paul 493* (US); *Pittier 2357* (US). PROVINCE UNKNOWN: *Duke* 1523 (MO).

4. **Pseuderanthemum standleyi** Leonard, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1246. 1938. TYPE: Costa Rica, *Standley & Valerio 49481* (US, not seen).

Herbs to 40 cm tall; stems terete, puberulous along 2 lines. *Leaves* ovate lanceolate, to 8 cm long, 3 cm wide, apically acuminate, basally attenuate, gla-

brous to sparingly strigose above, puberulous beneath mostly at the costa and the veins, the cystoliths dense, moderately prominent on both the surfaces, the margins undulate; petioles short, 1–3 mm long, puberulous. *Inflorescences* in terminal spicate panicles and in axillary spikes, the spikes lax to 9 cm long, the rachises glandular puberulous; bracts and bracteoles subulate, to ca. 3 mm long, 0.5 mm wide basally, glandular puberulous; pedicels mostly borne singly or in clusters of 2, alternate on the rachis. *Flowers* with the calyx 5-merous, segments narrowly subulate, to 5 mm long, 0.5 mm wide, glandular puberulous; corolla purplish, sparingly and minutely puberulous, the tube ca. 15 mm long, 1 mm in diameter, lobes of the limb elliptic, ca. 7 mm long, 3.5 mm wide, apically obtuse; stamens included, the staminodes slightly longer than the filaments. *Capsules* ca. 15 mm long, 2.5 mm wide, 2 mm thick, glabrous; seeds 4, oblique, flattened, 3 mm long, 2 mm wide, roughened.

This species grows in moist thickets and open areas at elevations above 1,000 m in Costa Rica and adjacent Panama. A Mexican specimen, *Hinton* 8865 (MO), has been observed.

CHIRIQUÍ: Jaremillo, Boquete District, 5000 ft, *Terry 1284* (MO).

26. RAZISEA

Razisea Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1854: 142. 1854. TYPE: *R. spicata* Oersted.

Shrub. Leaves mostly glabrous elliptic. *Inflorescences* are in terminal and axillary thyrses which superficially resemble spikes, the bracts and the bractlets small and inconspicuous; flowers either sessile or pedicellate. *Flowers* with the calyx 5-merous with equal lobes, the corolla bilabiate, the upper lip narrow, the lower lip broad and 3-lobed at the tip; stamens 2, exserted, the filaments flattened, the anthers 1-celled; style exserted, the stigma 2-parted. *Capsules* clavate, 4-seeded.

The genus consists of one species.

1. **Razisea spicata** Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1854: 142. 1855. TYPE: Costa Rica, *Oersted 1500* (C, not seen).—FIG. 26.

A *shrub* to 2 m tall; stems quadrangular in the young portions, glabrous. *Leaves* elliptic to slightly ovate, to 22 cm long and 8.5 cm wide, apically acuminate, basally attenuate, glabrous above, glabrous to puberulous along the midrib and the costa beneath, cystoliths numerous and visible on both the surfaces, the margins entire to slightly crenate, the petioles varying from subsessile to 4 cm long, glabrous. *Inflorescences* in terminal and axillary thyrses to 27 cm long; rachis puberulous to sericeous, the bracts one per flower, small, subulate, to 3 mm long, 1 mm wide at the base, puberulous, the bractlets 2, subulate, slightly smaller than the bracts; pedicels borne singly and in fascicles of 2 or 3, puberulous, to 3 mm long. *Flowers* with the calyx 5-merous, the lobes equal, linear, to 5 mm long, 0.5 mm wide at the base, puberulous; corolla bright red, funnelform, ascending, slightly curved to one side, to 4 cm long, to 9 mm wide at the mouth, 2

FIGURE 26. *Razisea spicata* Oerst. Habit (×½). [After *Wedel* 2574 (MO).]

mm wide at the base, glabrous, bilabiate, the upper lip linear to 8 mm long, 4 mm wide at the base, apically rounded, ciliolate, the lower lip with 3 small acute lobes at the tip, the lobes about equal, 1 mm long, the lower lip, when open forming an oblique angle from the upper lip; stamens exserted, the filaments to 4.5 cm long, glabrous, the anther cell to 3 mm long, the base rounded. *Capsules* (Leonard 1938) to 17 mm long; glabrous, seeds roughened.

This species is found in rain forests of Costa Rica, Panama and Colombia. Capsules were not seen on Panamanian specimens.

BOCAS DEL TORO: Along road between Almirante and Ojo de Agua 3–6 km W of Almirante, 30–200 m, *Croat 38202* (MO). Changuinola Valley, *Dunlap 111* (US). Río Teribé, between Quebrada Treglo and Puerto Palenque, 90–105 m, *Kirkbride & Duke* 535 (MO). Rain forest by river, Chiriquicito to 5 mi S along Río Guarumo, *Lewis et al. 2033* (MO).

Water Valley, Chiriquí Lagoon, *Wedel 644, 1427, 1601, 2574* (all MO). CANAL ZONE: Río Providencia 3 km SE of Achiote near W border of Canal Zone, 5–100 m, *Gentry & Nee 8651* (MO). Río Providencia and ridge S of river, 5–170 m, *Gentry & Nee 8708, 8745* (both MO). CHIRIQUÍ: Cerro Punta, 2000 m, *Allen 1514* (US). Palo Santo, 3 mi N of Volcán, *Croat 13596* (MO). Frequent in ravine W of Cerro Pando, *D'Arcy 6620* (MO). Woods around Alto Lino, 4000–5000 ft, *Maurice 844* (MO). Santa Clara region, 27 km NW of El Hato de Volcán, on coffee finca of Rattibor Hartman called Ojo de Agua, 5000–5300 ft, *Mori & Bolten 7201* (MO). Cerro Colorado, 50 km N of San Felix on the Continental Divide, 1200–1500 m, *Mori & Dressler 7862* (MO). N of San Felix, 37.2 km by road from the Interamerican Highway, *Mori & Kallunki 5998* (MO). COCLÉ: El Valle, 600–1000 m, *Allen 1219* (MO). La Mesa N of El Valle, *Allen 2790, 3685* (both MO). DARIÉN: Santa Fé, forested slope of Cerro Tute, 3000 ft, *Allen 4342* (MO). Along Panamerican Highway between Pucro and Río Punusa, *Duke 5399* (MO). 10 mi S of El Real on Río Pirre, *Duke 5426* (MO). Camino del Pirre, *Duke & Bristan 257* (DUKE). PANAMÁ: Cerro Trinidad, SE slope, *Kirkbride & Duke 1681* (MO). SAN BLAS: Cuna Reservation, Río Morti, 6 mi upstream from Morti Arriba, 160–260 ft, *Duke 8450* (MO). VERAGUAS: 5 mi W of Santa Fé on road past Escuela Agrícola de Alto Piedra on Pacific side of divide, 800–1200 m, *Croat 23038b* (MO). Valley of Río Dos Bocas, 11 km from Escuela Agrícola Alto Piedra (above Santa Fé) on road to Calovébora, 450 m, *Croat 27482* (MO). Cerro Tute, ca. 10 km NW of Santa Fé, 750–1000 m, *Mori et al. 7949* (MO). NW of Santa Fé, 1 km from Escuela Alto de Piedra, *Mori & Kallunki 4869* (MO).

27. RUELLIA

Ruellia L., Sp. Pl. 634. 1753; Gen. Pl., ed. 5. 283. 1754. LECTOTYPE: *R. tuberosa* L.

Dipteracanthus Nees in Wallich, Pl. Asiat. Rariores 3: 81. 1832. LECTOTYPE: *D. prostratus* (Poiret) Nees.
Aphragmia Nees in Lindl., Nat. Syst. ed. 2. 444. 1836. TYPE: *A. haenkei* Lindl.
Arrhostoxylum Nees in Mart., Fl. Bras. 9: 57. 1847. LECTOTYPE: *A. glabrum* Nees.

Perennial *herbs* or *shrubs*. *Leaves* petiolate, elliptic, ovate, ovate lanceolate, oblong spathulate, acuminate or obtuse, the margins entire, slightly undulate or repand crenulate. *Flowers* often large and showy, borne either singly or in various inflorescence forms which are either terminal or axillary or both, regular, sometimes curved, pedicellate; bracts one or absent; bracteoles 2 or absent. *Flowers* with the calyx 5-merous, mostly equal; corolla red, yellow, white or purple, funnelform, salverform or sometimes saccate, the tubes usually narrow and the expanded portion often campanulate, with five spreading, obtuse lobes; stamens four, didynamous, the anthers 2-celled, muticous at the base; stigma lobes unequal. *Capsule* oblong or clavate, the dissepiment remains attached to the capsule wall at maturity; seeds flattened with a rim of sticky mucilaginous hairs when wet, glabrous when dry.

This genus is worldwide and it occurs in both tropical and temperate regions.

a. Corolla over 8 cm long; calyx segments over 3 cm long ..... 15. *R. praeclara*
aa. Corolla under 8 cm long; calyx segments under 3 cm long.
  b. Inflorescences spicate or in headlike clusters terminating the peduncles; bracts over 2 cm long.
    c. Inflorescences in headlike clusters terminating the peduncles; corollas under 3 cm long.
      d. Corolla white or bluish; stamens included ..... 2. *R. biolleyi*
      dd. Corollas red; stamens exserted.
        e. Leaves ovate, over 4 cm wide; bractlets to 6 mm long, apically acute ..... 5a. *R. fulgida* var. *fulgida*
        ee. Leaves ovate-lanceolate, under 3.5 cm wide; bractlets to 15 mm long, apically rounded ..... 5b. *R. fulgida* var. *angustissima*

cc. Inflorescences spicate; corollas over 3 cm long.
f. Inflorescences in short terminal spikes ca. 1 cm long; bracts, leaves, and calyx gland dotted.
g. Flowers red ..... 17a. *R. tubiflora* var. *tubiflora*
gg. Flowers white ..... 17b. *R. tubiflora* var. *tetrasticantha*
ff. Inflorescences in spikes over 5 cm long; bracts, leaves, and calyx not gland dotted.
h. Corolla black or purplish black; calyx over 20 mm long ..... 1. *R. anthracina*
hh. Corolla red or white; calyx under 15 mm long.
i. Corolla red; bracts green, leaflike ..... 3. *R. colonensis*
ii. Corolla white; bracts white or yellowish white, spatulate ..... 8. *R. leucobracteata*
bb. Inflorescence paniculate, flowers borne on simple or dichotomously branched peduncles or flowers solitary or in clusters of 2–4 at the leaf axils or the stem tip; bracts under 2 cm long.
j. Calyx fused for ⅔ of its length, campanulate; corolla red ..... 9. *R. macrophylla*
jj. Calyx not fused or fused for less than ½ its length; corolla white, pink or purplish, but not red.
k. Calyx with one segment conspicuously longer than the others ..... 7. *R. inundata*
kk. Calyx with segments equal or nearly so, but none conspicuously longer than the other.
l. Capsules cylindric or elliptic; branches of inflorescence glandular puberulous.
m. Leaves ovate to elliptic; stamens slightly exserted ..... 13. *R. paniculata*
mm. Leaves oblong spatulate; stamens included ..... 12. *R. nudiflora* var. *puberula*
ll. Capsules clavate; branches of inflorescence, if present, eglandular.
n. Flowers solitary or in clusters of 2–4 at the leaf axils or stem tip; capsules under 11 mm long.
o. Axillary flowers borne singly or in pairs; bracts absent ..... 6. *R. geminiflora*
oo. Axillary flowers in clusters of 3–4; bracts linear, ca. 7 mm long ..... 11. *R. metallica*
nn. Flowers in panicles of simple or dichotomously branched peduncles; capsules over 11 mm long.
p. Corolla over 3.5 cm long; capsule over 2 cm long ..... 10. *R. malacosperma*
pp. Corolla under 3 cm long; capsule under 2 cm long.
q. Flowers fascicled at the ends of long peduncles; calyx segments over 20 mm long ..... 2. *R. biolleyi*
qq. Flowers solitary at the ends of peduncles or borne in dichotomously branched cymes; calyx segments under 10 mm long.
r. Capsules glabrous; corolla mauve or purplish.
s. Peduncles mostly over 10 cm long; bracts oblong-spatulate. ..... 14. *R. pittieri*
ss. Peduncles mostly under 10 cm long; bracts linear oblong ..... 16. *R. tonduzii*
rr. Capsules puberulous or glandular puberulous; corolla white ..... 4. *R. cooperi*

1. **Ruellia anthracina** Leonard, Proc. Biol. Soc. Wash. 56: 53–56. 1943. TYPE: Panama, *Allen 2732* (US).—FIG. 27.

Herbs, suffrutescent, to 2 m high; stems quadrangular, puberulous when young. *Leaves* elliptic to 25 cm long and 11 cm wide, the apex acuminate and the base attentuate, glabrous except for puberulence beneath along the costa and

FIGURE 27. *Ruellia anthracina* Leonard.—A. Habit (×⅜).—B. Corolla (×1). [After *Dwyer et al. 4540* (MO).]

major branches, the margins entire; petiole 1–3 cm long. *Inflorescences* in terminal and axillary spikes to 45 cm long; pedicels ca. 2 mm long, the 1 bract subtending each flower elliptic to obovate, to 5.6 cm long, 1.6 cm wide, acuminate at the apex, acute at the base, puberulous on both the surfaces, entire; 2 bractlets subtending each flower, oblanceolate, to 3.5 cm long and 3 mm wide, puberulous to puberulous glandular on both the surfaces. *Flowers* with the calyx 5-merous, linear to 27 mm long, ca. 1 mm wide, puberulous to puberulous glandular outside, sparingly puberulous inside; corolla black to purplish black, infundibular, curved, to 6.5 cm long with numerous small glandular hairs outside, glabrous inside, the 5 lobes each ca. 6 mm wide, each lobe divided apically by a rounded notch; stamens 4, didynamous, included, the anthers 2-celled, 0.65 mm long, blunt at the base; ovary of mature flower oblong, flattened with enlarged base, 0.5 mm long, 0.14 mm wide, wooly at the apex and along the two margins, velutinous elsewhere, the style pilose. *Capsule* clavate to 25 mm long, 8 mm wide, pilose, containing up to 8 flat, orbicular seeds ca. 53 mm in diameter, rimmed with mucilaginous hairs when wet, glabrous when dry, dark brown in color.

Found in wet areas in clearings or along tracts of rain forest and swampy areas adjacent to streams and shore, *Ruellia anthracina* is most similar to *R. tubiflora*. It differs in color of flower, inserted stamens, longer corolla, conspicuous glandular hairs on the corolla, the calyx and the bracteoles.

COCLÉ: Hills above El Valle de Antón, *D'Arcy 6771* (MO). Cerro Pilon, above El Valle de Antón, rain forest, 2000–2700 ft, *Dwyer et al. 4540* (MO). Hills above El Valle, ca. 1000 m, *Gentry 6876* (MO). El Valle site area of WEPCOR, Cerro Pilon, *Kirkbride 1051* (MO). Trail from La Mesa towards Los Llano and the border between provinces of Coclé and Panamá, *Luteyn 4108* (DUKE). PANAMÁ: 16 km above Panamerican Highway on road from El Llano to Cartí-Tupile, *Kennedy et al. 2447* (MO). VERAGUAS: Mouth of Río Concepción, beach, *Lewis et al. 2809* (MO).

2. **Ruellia biolleyi** Lindau, in Pittier, Primit. Fl. Costaric. 2: 301. 1900. TYPE: Costa Rica, *Biolley 73961* (B?, not seen).

Herbs, sometimes suffrutescent, erect, to 1.0 m tall; stem quadrangular, sharply angled or slightly winged, wooly to villous when young. *Leaves* elliptic, 8–15 cm long, 3–5 cm wide, apically acuminate, basally attenuate, glabrous, darker above, often purplish, green beneath, the margins entire to slightly undulate; petiole 1–4 cm long. *Inflorescences* in axillary cymes, the peduncle to 18 cm long; pedicels ca. 2 mm long, white to purplish; bracts and bractlets small, ca. 5 mm long, lanceolate to spatulate. *Flowers* with the calyx and the pedicel covered with glandular hairs, 4–6 mm long; corolla to 2.5 cm long, the lower portion of tube 1 mm wide, 5 mm wide at the throat, the lobes rounded, ca. 5 mm wide, puberulent outside, villous inside at the throat; stamens included, the anthers rounded at the base. *Capsule* ca. 12 mm long, 3 mm wide, apically pointed and basally narrowed, the surface with glandular hairs; seeds 4–5, flat, ca. 1.8 mm in diameter.

This species is found in rain forests of Panama and Costa Rica.

BOCAS DEL TORO: Region of Almirante, Daytonia Farm, *Cooper 185* (NY), *Lewis et al. 2056* (MO). Almirante Bay, *Wedel 11* (MO). Locality unknown, *Wedel 168* (MO). Water Valley, *Wedel 748* (MO). Chiriquí Lagoon, *Wedel 2562* (MO). Nievecita, ca. 0–50 m, *Woodson et al. 1805* (MO). COLÓN: Río Guanche, *Gentry 6309* (MO). DARIÉN: Headwaters of Río Chico, 500–750 ft, *Allen 4624* (MO). Cabecero del Río Pirre, *Bristan 1307* (MO). Río Pirre, 2–5 mi above El Real, *Duke 5072* (MO). Río Pirre, near crossing of trail from El Real to Tucuti, 20 mi W of El Real, *Duke 5188* (MO). Río Chíco, across from Boca de Tosca along the top of ridge, *Duke 5215* (MO). Forest 1–4 mi N of Pucro, *Duke 13034* (MO). Trail from Río Pucro to Quebrada Maskia, *Duke 13079* (MO). Interamerican Highway, ca. 1 mi SE of Río Turia, *Duke 14558* (MO). Forest 1–3 mi N of Paya, *Duke & Kirkbride 14012* (MO). Near Cerro Pirre base camp on Río Perasenico, 200–500 m, *Gentry & Clewell 7059* (MO). Quebrada "Camachimuricate" cerca casa de Bartolo, *Kennedy 2837* (MO). Boca de Pauarando, on Sambú River, southern Darién, 20 m, *Pittier 5583* (F). Foothills of Garagara, Sambú basin, southern Darién, 30–500 m, *Pittier 5622* (US).

3. **Ruellia colonensis** Wasshausen, Phytologia 33: 59. 1976. TYPE: Panama, *Dwyer & Gentry* 9371 (US).

Herb to 0.5 m tall; younger stems quadrangular, pilose to subtomentose, the hairs appressed, brown, to 1.5 mm long. *Leaves* ovate to ovate elliptic, 13.5–20 cm long, 4.5–7.5 cm wide, apically acuminate, basally cuneate, glabrate above, sparingly to densely pilose beneath, especially the costa and the lateral veins, the hairs appressed to ascending, ca. 0.3 mm long, the veins prominent beneath, the cystoliths relatively obscure, the margins undulate or crenate serrate; petioles 4–5 cm long, hairs as on the stem. *Inflorescences* in terminal and subterminal spikes, to 12 cm long, 3 cm wide excluding corollas, the flowers sessile to subsessile; bracts conspicuous, lanceolate, leaflike, 2–3 cm long, 5–6 mm wide, the lowermost somewhat larger, apically acuminate, glandular pilose, ciliate, hairs to 1.25 mm long, ascending, the bractlets oblong to oblanceolate, 1.2 cm long, 1.8–2 mm wide, apically subacute to subobtuse, the hairs as on the bracts. *Flowers* with the calyx segments narrowly lanceolate, subequal, 16 mm long, 1.8–2 mm wide, apically acuminate, glandular-pilose and puberulous outside, puberulous inside, densely ciliate with glandular hairs; corolla bright red, 5.5–6.5 cm long, sparingly pilose, the tube curved, 2.5 mm wide at the base, narrowing to 2 mm just above the ovary, enlarging gradually to 11 mm wide at the mouth, the limb 1.5 cm broad, the lobes suborbicular, 3 mm in diameter; stamens barely included to slightly exserted, 18 mm long, the anthers oblong, 5 mm long, 1.3 mm wide, rounded at both ends, the filaments glabrous above, puberulous at the base. *Capsule* elliptic, ca. 15 mm long, 6 mm wide, 4.5 mm thick, glabrous; seeds 2–4, oval, flattened, 4.5 mm long, 3.5 mm wide, glabrous, with a rim of minute mucilaginous hairs when moistened.

COLÓN: Santa Rica lumber road, E of Colón, *Dressler 3356* (MO). Santa Rita Ridge, *Dwyer & Gentry 9371* (US).

4. **Ruellia cooperi** Leonard, Field Mus. Nat. Hist., Bot. 18: 1251. 1938. TYPE: Panama, *Cooper 185* (F).

Herb, sometimes suffrutescent, to ca. 50 cm tall; stems quadrangular, the angles winged, the cystoliths dense, glabrous. *Leaves* elliptic, 8–16 cm long, 2.5–5.5 cm wide, apically acuminate, basally attenuate, glabrous above with strigose hairs on the costa and the lateral veins beneath, the cystoliths dense and prom-

inent on both the surfaces, the margins entire to undulate; petioles 1–3.5 cm long, puberulous. *Inflorescences* of peduncled, axillary, dichotomously branching panicles, the peduncles to 30 cm long, sharply quadrangular, glabrous, the branches frequently curving. *Flowers* solitary or in pairs borne at the axils or terminating the branches, the pedicels to 4 mm long, glandular puberulous; bracts spatulate, 3–5 mm long, 1–1.5 mm wide; calyx 6–7 mm long, the segments subulate, 4–5 mm long, 0.75 mm wide at the base, glandular puberulous; corolla white, sparingly puberulous, 2.5–2.8 cm long, the tube 1.5 mm in diameter for ca. 11 mm then expanding obliquely to 8 mm wide at the mouth, the limb 8–12 mm broad, the lobes rounded, 4.5–5 mm in diameter; stamens included. *Capsules* clavate, ca. 15 mm long, 3 mm broad, 2 mm thick, retrorse puberulous and with occasional glandular hairs, the stipe ca. 7 mm long; seeds discoid, ca. 2 mm in diameter.

This species is known only from the type collection in Panama. The habitat was not described except for the locality near sea level.

This species resembles *R. pittieri*, but can be distinguished from it by its puberulous capsule. It also resembles *R. biolleyi*, but differs from it in the more extensive branching of the inflorescence.

BOCAS DEL TORO: Daytonia Farm, Almirante region, *Cooper 185* (F, holotype).

5. **Ruellia fulgida** Andr., Bot. Rep. 8: *tab.* 527. 1808. TYPE: Cultivated from collected material of the West Indies.

Arrhostoxylum fulgidum (Andr.) Nees in Mart., Fl. Bras. 9: 59. 1851.

5a. **Ruellia fulgida** Andr. var. **fulgida**.

Herbs, sometimes suffrutescent, erect to 2 m high; stems quadrangular, glabrous. *Leaves* ovate, 6–25 cm long, 2.8–9.0 cm wide, apically acuminate, basally attenuate, glabrous, the cystoliths numerous and conspicuous on both the surfaces giving a mottled gray cast to the leaves, the margins entire to slightly crenulate; petioles to 4.5 cm long. *Inflorescences* in dense headlike clusters terminating a peduncle to 10 cm long with some axillary flowers as well; bracts subtending the heads and the solitary flowers lanceolate, to 3 cm long and 0.6 cm wide; bractlets triangular to oblanceolate, to 6 mm long, apically acute; flowers sessile, several to 10 or more per head. *Flowers* with the calyx to 6.5 mm long, puberulent, the corolla puberulent toward the base, the tube funnelform to 2.5 cm long, 4.5 mm wide at the mouth and 0.7 mm wide at the base, the lobes to 8 mm long and 4 mm wide, rounded at the tip; stamens exserted to ca. 5 mm beyond the mouth, the anthers oblong, blunt at the base. *Capsule* ca. 12 mm long, 3 mm wide, obovate, pointed at the tip, narrowed at the base; seeds 6–8, flat, oval, 2.6 mm in diameter.

This species is found in damp thickets or woods.

CANAL ZONE: Indio, Madden Lake, *Miller 2057, 2076* (both US). COCLÉ: El Valle de Antón, *Maurice 769* (US). DARIÉN: Río Sabana, *Leopold 138* (MO). HERRERA: Ocú, banks of Río Pasoancho, *Stern et al.* 33597 (US).

5b. **Ruellia fulgida** var. **angustissima** (Hochr.) Leonard, Contr. U.S. Natl. Herb. 31(1): 68. 1951. TYPE: Colombia, *Holton* 599 (NY).

Arrhostoxylum fulgidum Nees var. *angustissimum* Hochr., Bull. New York Bot. Gard. 6: 287. 1910. TYPE: Colombia, *Holton* 599 (NY).

This variety differs from the typical *R. fulgida* collections in its narrower ovate lanceolate leaves to 9 cm long and 3.5 cm wide, shorter petioles to 3 cm long, and longer bractlets to 1.5 cm long, which are mostly rounded at the tips, and are oblanceolate.

This species is found along trails in damp thickets or wooded areas. It ranges from Panama to Colombia and Venezuela.

COCLÉ: El Valle de Antón, N rim, 600–1000 m, *Allen 1661* (MO). Río Indio trail, 500–700 m, *Hunter & Allen 323* (MO).

6. **Ruellia geminiflora** H.B.K., Nov. Gen. Sp. Pl. 2: 240. 1817. TYPE: Colombia (not seen).

Dipteracanthus geminiflorus (H.B.K.) Nees in Mart. Fl. Bras. 9: 40. 1847.

Ascending *herbs* to ca. 30 cm high; stems quadrangular, sparingly to densely pilose. *Leaves* ovate to ovate elliptic, 2–5 cm long, 0.8–1.8 cm wide, apically acute, basally attenuate, the cystoliths densely distributed over the upper surface, glabrous to puberulous above, glabrous to densely puberulous beneath, the margins entire to crenulate; mostly sessile; pedicels axillary borne singly and in pairs, ca. 1.0 mm long. *Flowers* with the calyx lobes equal, subulate, to 8 mm long, ca. 0.8 mm wide at the base, mostly pilose to densely pilose; corolla mauve, funnelform, tube 25 mm long, 2 mm wide at the base, 8 mm wide at the mouth, puberulous outside, glabrous inside, the limb ca. 25 mm across, the lobes equal, suborbicular, ca. 10 mm in diameter, puberulous on both the surfaces; stamens included, the filaments glabrous; ovary and style puberulous. *Capsule* clavate, ca. 8 mm long, 3.5 mm wide and 2 mm thick, puberulous; seeds 4, orbicular, flattened, ca. 3 mm across.

This species is found in open, grassland areas of Central America, the West Indies and northern South America.

CANAL ZONE: Monkey Hill, *Cowell 23* (NY), *Greenman & Greenman 5095* (MO). Ancón Hill, *Piper 5541* (US). Chiva-Chiva Trail, Red Tank to Pueblo Nuevo, *Piper 5761* (US). Sosa Hill, Balboa, *Standley 26435* (US). COCLÉ: *Williams 379* (NY). PANAMÁ: Cerro Campana, 1000 m, *Allen 2441* (US). Between Río Pacora and Chepo, roadside savanna, *Dwyer et al. 5098* (MO). Tapia River, *Killip 3306* (US). Juan Diaz Region near Tapia River, *Maxon & Harvey 6623* (US). Sabanas N of Panama City, *Paul 403* (US). Laguna de Portala near Chepo, *Pittier 4595* (US). Sabanas, *Standley 25909* (US). Near Punta Paitilla, *Standley 26300* (US). Near big swamp E of Río Tocumen, *Standley 26603* (US). Tumba Muerto road near Panamá, *Standley 29749* (US). Río Tapía, *Standley 41179* (US).

7. **Ruellia inundata** H.B.K., Nov. Gen. Sp. Pl. 2: 239. 1817. TYPE: Colombia (not seen).

R. albicaulis Bertero in Spreng., Syst. 2: 822. 1825. TYPE: Colombia (not seen).
Aphragmia haenkei Nees in Lindl., Nat. Syst., ed. 2. 444. 1836. TYPE: Mexico, *Haenke* (not seen).

Dipteracanthus haenkei Nees in DC., Prodr. 11: 141. 1847. SYNTYPE: Panama, *Cuming 1163* (MO).
Aphragmia inundata (H.B.K.) Brem., Verh. Kon. Nedl. Akad. Wetensch. Amsterdam, Afd. Natuurk. Tweede Sect. 2, 45, no. 1: 10. 1948.

Herbs, sometimes suffrutescent, erect to 1.5 m; younger stems quadrangular and puberulent or puberulent glandular and with scattered long hairs, the older stems scattered pilose to glabrous. *Leaves* ovate to ovate lanceolate, to 15 cm long and 7.5 cm wide, apically acuminate, basally acute to attenuate, dense to sparingly hispidulous on both the surfaces, the margins repand crenulate, sometimes entire in the smaller leaves; petiole to 8 cm long, pilose. *Inflorescences* axillary, ascending, dichotomously branched, often forming a dense panicle, glandular pubescent; bracts to 9 mm long and 3 mm wide; flowers sessile. *Flowers* pink to purplish, with the calyx to 1.7 cm long, glandular pubescent, the segments linear with one segment conspicuously longer than the rest; corolla to 2.5 cm long, 1.5 cm across at the limb, the lobes to 5 mm wide, rounded; stamens included. *Capsule* clavate and flattened, to 8 mm long, glabrous, 2–4 seeded.

This species is found in dry or moist soil along roadsides, in pastures and along streams. It ranges through Mexico, Central America, Colombia and Brazil.

CANAL ZONE: TTC Albrook Tower out C-15 road, *Blum 2171* (MO); *Dwyer & Robyns 101* (MO). Madden Dam, *Dwyer 5044* (MO). Boy Scout Road, *Dwyer 8392* (MO). Madden Forest along Las Cruces Trail, 75 m, *Hunter & Allen 675* (MO). Boy Scout Road, Madden Dam area, second growth forest, *Porter et al. 4004, 4024* (both MO). Pueblo Nuevo, *White 301* (MO). COCLÉ: Banks of Río Grande, *Burch et al. 1174* (MO). Weedy pasture 3 mi NE of Antón, *Croat 9629* (MO). Wet bank by stream, 3 mi NE of Antón, *D'Arcy & Croat 4113* (MO). Chigoré Penomoné, *Puga 46* (MO). HERRERA: Vic. of Ocú, 100 m, *Allen 4041* (MO). Banks of Río Santa María, *Burch et al. 1203* (MO). Road from La Avena to outskirts of Pesé, ca. 200 ft, *Burch et al. 1306* (MO). ½ mi NE of Ocú, open pasture, *Stern et al. 1711* (MO). 4 mi S of Los Santos, moist area in pasture, *Tyson 2688* (MO). 10 mi S of Ocú along road, *Tyson et al. 2828* (MO). LOS SANTOS: Roadside, 7 mi S of Chitré, *D'Arcy & Croat 4174* (MO). Roadside, 2 mi E of Chitré, *D'Arcy & Croat 4193* (MO). Between Pacora and Chepo, *Dressler 3938* (MO). Punta Mala, moist land, *Tyson 2705* (MO). PANAMÁ: Between Río Pecora and Chepo, *Dressler 3938* (DUKE); *Dwyer et al. 5099* (MO). PROVINCE UNKNOWN: *Cuming 1163* (MO); *Denham s.n.* (MO).

8. **Ruellia leucobracteatus** Durkee.[13] TYPE: Panama, *Croat 16843* (MO, holotype).

Shrub to 1.5 m tall; stems subquadrangular in younger portions, the angles rounded, puberulous. *Leaves* elliptic to elliptic obovate, to 24 cm long, 7.5 cm wide, apically acuminate, basally attenuate, glabrous, the cystoliths ca. 0.3 mm

[13] *Ruellia leucobracteatus* Durkee, sp. nov. Frutex ad 1.5 m alta; foliis ellipticis ad obovato-ellipticis, ad 24 cm longis, 7.5 cm latis, glabris, cystolithis crebris, utrinque prominentibus, ca. 0.3 mm longis, marginibus undulatus; inflorescentibus terminalibus ex spicis ca. 10 cm longis, 1.5 cm latis constantibus, bracteis spathulatis, imbricatis, supra basim in sicco alba vel eburnea, ad 2.5 cm longis, 8 mm latis, puberulo-glandularis, bracteolis anguste oblanceolatis, 2 cm longis, 2 mm latis, minute puberulo-glandularis; corolla alba, infundibulari, puberula, ad 3.7 cm longa; staminibus inclusis.

long, dense, prominent on both the surfaces, the margins undulate; petioles to 3.5 cm long, glabrous. *Inflorescences* in terminal spikes ca. 10 cm long, 1.5 cm wide; rachis quadrangular, puberulous; bracts spathulate, imbricate, white or yellowish white above the base upon drying, to 2.5 cm long, 8 mm wide, apically acute, puberulous glandular; bracteoles narrowly oblanceolate, 2 cm long, 2 mm wide, minutely glandular puberulous. *Flowers* with the calyx lobes linear lanceolate, 13 mm long, 1.25 mm wide, puberulous, the margins ciliolate; corolla white, funnelform, to 3.7 cm long, puberulous, the tube basally 2.5 mm broad, expanding to 6 mm at the mouth, curving to one side, the lobes suborbicular, ca. 5 mm in diameter; stamens included, puberulous. *Capsule* clavate, reddish brown, puberulous, 13 mm long, 6 mm wide, 3 mm thick; seeds 8, orbicular, flattened, ca. 3 mm in diameter, the margins puberulous.

This species was found in rain forest at sea level near the Colombian border. Corollas on the one specimen observed did not appear to be fully mature.

SAN BLAS: Forest SE of Puerto Obaldía, *Croat 16843* (MO).

9. **Ruellia macrophylla** Vahl, Symb. Bot. 2: 72. 1791. TYPE: Colombia, *Vahl* (C, not seen; microfiche, MO, photo, US).

Stemonacanthus macrophyllus (Vahl) Nees in DC. Prodr. 11: 205. 1847.

Herbs to small *shrubs*; stems erect, quadrangular, glabrous to puberulous. *Leaves* elliptic to ovate elliptic, 8–20 cm long, 2–6 cm wide, apically acuminate, basally acute, glabrous on both the surfaces, the cystoliths dense and visible on both the surfaces, the margins undulate or shallowly crenate; petioles 0.5–2 cm long, glabrous to sparingly puberulous. *Inflorescences* in axillary peduncled cymes, the peduncles subquadrangular, to 13 cm long, glabrous, often with flowers in the forks; bracts subtending the flowers lanceolate, 2–16 mm long, 1–2 mm wide, those subtending the branches of the inflorescence somewhat larger, all glabrous; pedicels 1–3 mm long, glabrous. *Flowers* with the calyx campanulate, 7–9 mm long, coalesced for ca. ⅔ of its length, the lobes subulate to subulate linear, of unequal lengths, 2–4 mm long, sparingly puberulous, the margins minutely ciliolate; corolla red, to 4 cm long, sparingly puberulous, the tube salverform, to 3 cm long, 2 mm wide at the base, 6.5 mm wide at the mouth, the lobes oblong, ca. 10 mm long, 5 mm wide, apically rounded; stamens exserted, the anthers 3 mm long, 1.5 mm broad, short spurs ca. 0.25 mm long at the base of each cell, the filaments glabrous; ovary glabrous, the style puberulous. *Capsules* clavate, 14 mm long, 4 mm broad, the stipitate base 4–5 mm long, glabrous, 16-seeded; seeds reddish brown, lenticular, 3 mm broad.

This species is found in moist, often shady areas in forests and thickets, often along streams. It ranges from Panama to the West Indies, Colombia, Venezuela, Brazil and Peru. The capsule and seed descriptions were obtained from Leonard (1953).

DARIÉN: Púcuro, 70 m, *Mori & Gentry 4244* (MO).

10. **Ruellia malacosperma** Greenm., Proc. Amer. Acad. Arts 34: 572. 1899. TYPE: Mexico, *Pringle 6806* (location unknown, not seen).

Herbs to 50 cm tall; stems subquadrangular, glabrous to sparingly pilose. *Leaves* narrowly elliptic, 5–13 cm long, 1–3 cm wide, apically acute or obtusish, basally attenuate, both the surfaces glabrous or sparingly pilose along the costa and the basal margins, the cystoliths dense and conspicuous above and beneath, the margins entire or undulate; petioles to 2 cm long, sparingly long pilose. *Inflorescences* axillary, in once or twice dichotomously branched cymes, the peduncles to 8 cm long, glabrous, bearing conspicuous cystoliths; bracts linear, ca. 1 cm long, 1.5 mm wide at the base, uppermost smaller, all glabrous. *Flowers* with pedicels 5–15 mm long; calyx 13–15 mm long, divided nearly to the base, the segments subulate, 1.25 mm wide at the base, the margins sparingly glandular puberulous; corolla purple, 4–5.5 cm long, puberulous, tube 4 mm broad at the base expanding to 3 cm broad at the mouth, the throat funnelform, ventricose, the limb 4 cm broad, the lobes oval, ca. 1.5 cm in diameter; stamens included. *Capsules* narrowly clavate, 2.5–3 cm long, 6 mm broad, glabrous; seeds 8–20, discoid, ca. 3 mm in diameter, silky with white, appressed hairs when dry, mucilaginous pilose when wet.

This species is cultivated through much of the American tropics as it is in Panama.

PANAMÁ: Near the road from Calzada Larga at the "Maria Henriquez" dwellings, *Villamil 17* (MO).

11. **Ruellia metallica** Leonard, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1253. 1938. TYPE: Costa Rica, *Cook & Doyle 456* (US).

Suffrutescent *herb*, erect to 1 m high; stem quadrangular, glabrous or pilose at the angles. *Leaves* elliptic to elliptic ovate, to 15 cm long and 6.5 cm wide, apically acuminate and often curved, basally attenuate, glabrous above, sericeous beneath along the costa and the veins, the lower surface with a metallic sheen, the upper surface often purplish, especially the young leaves, the margins entire to shallowly undulate; petiolate to 2 cm long. *Inflorescences* axillary or terminal in small clusters of 3 or 4; bracts small, linear to 7 mm long, the bractlets smaller, triangular to ca. 2 mm long, puberulent. *Flowers* sessile, pink, or lilac; calyx to 8 mm long, glabrous except for scant puberulence along the margins of the lobes; corolla to 2.5 cm long, puberulent, narrow portion of tube to 1.1 cm long and 1.5 mm wide, the expanded portion obconical, 6 mm wide at the throat, the limb to 2 cm across, the lobes suborbiculate, to 7 mm in diameter; stamens included, glabrous. *Capsules* clavate to 1 cm long, 3 mm wide, minutely puberulent; seeds 2, ovate, ca. 2.8 mm long.

This species occurs in rain forests and wet thickets of Nicaragua, Costa Rica and Panama.

The variation in leaf coloration is pronounced and some specimens clearly display the metallic sheen on the underside of the leaves while in others this is

lacking, and there may be a dark, purplish coloration on the upper surface instead. Possibly this is due to variations in habitat.

BOCAS DEL TORO: Island Potrero, *Dunlap 461* (US). Water Valley, *Wedel 588, 667, 919* (all MO). Chiriquí Lagoon, *Wedel 1039, 2713* (both US). CANAL ZONE: Barro Colorado Island, *Croat 8642* (MO). COCLÉ: Boca del Toabre at confluence of Río Toabre and Río Cocle del Norte, advanced rain forest, *Lewis et al. 5525* (MO). COLÓN: Ridge top, 1–3 mi W of Portobelo, *Gentry 1749* (MO). Río Guanche, 1–4 km upstream from Portobelo Road, tropical wet forest, 0–100 m, *Gentry 8788* (MO). Forests of Portobelo, 5–200 m, *Maxon 5755* (US). DARIÉN: Cloud forest, Cerro Campamento, S of Cerro Pirre, *Duke 15602* (DUKE, US). PROVINCE UNKNOWN: Western Panama, cacao plantation, *Stork 34.5* (US).

12. **Ruellia nudiflora** (Engelm. & Gray) Urb. var. **puberula** Leonard, J. Wash. Acad. Sci. 17: 517. 1927. TYPE: Guatemala, *Deam 6318* (US, not seen).

R. puberula (Leonard) Tharp & Barkley, Am. Midl. Nat. 42: 17.

Herbs, erect, 9–21 cm high; stem quadrangular, tomentose especially toward the apex, sometimes pilose glandular. *Leaves* oblong spatulate, to 4.5 cm long and 2.2 cm wide, apically obtuse, basally attenuate, decurrent on the petiole, densely pilose on both surfaces in a mixture of long and short hairs, entire; petiole to ca. 1 cm. *Inflorescences* in axillary, paired cymes with a flower in the fork; peduncle to 4 cm long, densely pilose glandular with longer pilose hairs interspersed among minute, glandular hairs; bracts oblong to 7 mm long and 1.3 mm wide, tomentose; bractlets oblanceolate to 5 mm long; pedicels to 1 cm, pilose glandular. *Flowers* cream colored in bud, lavender when open; calyx to 1 cm long, densely pilose glandular, lobes linear and keeled, 1 mm wide at the base; corolla to 4 cm, puberulent inside and out, the narrow portion of tube to 12 mm long and 2.5 mm in diameter, broadly expanding at the throat to 15 mm across at the mouth, the limb to 3 cm across, the lobes suborbiculate to 1.3 cm in diameter, the margins undulate to entire; stamens included, glabrous. *Capsules* to 1.7 cm long, elliptic, 4 mm broad at the broadest point, 1 mm wide at the base, puberulous; seeds suborbicular, flattened, ca. 2 mm in diameter, 12 per capsule.

Found in dry savannas and pastures, this species survives burning and is then conspicuous for its showy flowers which appear close to the ground after growth is resumed. The fruit description was obtained from *Brenes 12547* (F), Costa Rica.

CANAL ZONE: Ancón Hill, *Greenman & Greenman 5117* (MO). COCLÉ: Weedy field near Santa Clara Beach, *Croat 9601* (MO). LOS SANTOS: Monagre beach road, ca. 2 mi from beach in dry savanna, *Lewis et al. 1687* (DUKE, MO). PANAMÁ: Between Chepo and El Llano, *Croat 14488* (MO).

13. **Ruellia paniculata** L., Sp. Pl. 2: 635. 1753. TYPE: Jamaica, Herb. Linn. (not seen).

Herbs or suffrutescent plants to 1 m tall; stems erect, ascending or procumbent and rooting at the nodes, subquadrangular, younger stems glandular puberulous, older portions glabrous. *Leaves* ovate to elliptic, 3–10(17) cm long, 1.5–4(6.5) cm wide, apically obtuse to acute, basally abruptly attenu-

uate, puberulous to glandular pubescent above, puberulous to hispidulous beneath, the cystoliths prominent on both the surfaces; margins undulate to crenate; petioles 0.5–4 cm long, pubescence that of the stem. *Inflorescences* axillary, dichotomously branched, divergent or ascending, the branches glandular puberulous; bracts leaflike, glandular puberulous; floral bracts linear elliptic, 4–8 mm long, 1–2 mm wide, glandular puberulent. *Flowers* with the calyx 1–1.5 cm long, glandular puberulent, the segments linear subulate, unequal; corolla blue, finely puberulous, 3–4 cm long, the lobes oval, 6–7 mm long, 5 mm broad, the limb 1–1.5 cm across; stamens slightly exserted. *Capsule* cylindric, 10–13 mm long, 2 mm in diameter, erect, apically attenuate, glabrous to sparingly puberulous toward the tip; seeds 8, flat, ovoid, 2 mm long, 1.5 mm wide, rimmed with mucilaginous hairs when wet.

Ranging from Mexico to northern South America, this species usually grows in dry, disturbed habitats at elevations of sea level to 200 m. No Panamanian collections of this species have been observed, but it is assumed that it grows there since it has been collected in adjacent areas of Costa Rica and Colombia.

COSTA RICA: Cañas, Guanacaste, *Daubenmire 682* (F).

14. **Ruellia pittieri** Lindau, Bull. Herb. Boissier, 5: 655. 1897. TYPE: Costa Rica, *Pittier 6743* (G, not seen).

Herbs, sometimes suffrutescent, to 1.5 m tall; stems quadrangular, winged, sparingly puberulous. *Leaves* elliptic to elliptic obovate, to 18.5 cm long and 5 cm wide, apically and basally attenuate, glabrous on both the surfaces or sericeous on the costa beneath, cystoliths prominent and dense on both the surfaces, ca. 0.5 mm long; margins entire to crenulate; petioles to ca. 1 cm long. *Inflorescences* in axillary panicles, the peduncles to 18 cm long, quadrangular, glabrous to sparingly puberulous; pedicels 3–10 mm long, glabrous; bracts linear to spatulate 3–8 mm long, the bractlets subulate ca. 1 mm long. *Flowers* with the calyx lobes linear, ca. 4 mm long and 0.5 mm wide at base, glabrous to sparingly puberulous; corolla mauve, funnelform, tube 15–20 mm long, 2 mm wide at base, 8 mm wide at the mouth, puberulous outside, sparingly villous at the throat, the lobes suborbicular, ca. 5 mm long and 5 mm across, mostly glabrous; stamens included; ovary and capsule glabrous. *Capsule* clavate, to 1.5 cm long, ca. 5 mm wide at the widest point, 1.5 mm wide at the base; seeds 4, orbicular, flattened, 3 mm in diameter, reddish brown.

This species is found in dense wet forests and thickets and along trails in such habitats in Costa Rica and Panama.

CHIRIQUÍ: Secondary forest along Quebrada Punta de Piedra, 2 mi SW of Puerto Armuelles, 0–100 m, *Croat 22446* (MO). Burica Peninsula, disturbed area above Quebrada Yerbazales, 200 m, *Croat 22600* (MO). Burica Peninsula, near Balsa, 12 mi S of Puerto Armuelles, *Liesner 189* (MO). COLÓN: Near Río Guanche, *Dressler 4057* (US). Semiswampy floodplain near bridge over Río Buenaventura, near Portobelo, *Foster 1698* (DUKE). Along Río Fato, 10–100 m, *Pittier 3900* (US). DARIÉN: Paya, Río Paya, trail between Paya and Payita, *Stern et al. 355* (US).

15. **Ruellia praeclara** Standley, Field Mus. Publ. Colombian Mus., Bot. Ser. 4: 263. 1929. TYPE: Panama, *Cooper 216* (F, holotype; NY, isotype).

Shrub to ca. 2 m tall; stem quadrangular in younger portions, terete below, glabrous when old, glabrous to sparingly appressed pilose when young, grooved. *Leaves* elliptic to elliptic oblanceolate, to 30 cm long, 9 cm wide, apically acuminate, basally attenuate, glabrous to sparingly strigose at the costa above, appressed pilose beneath, mostly at the costa and the veins, the cystoliths dense and prominent on both the surfaces, the costa and the veins raised and prominent beneath, the margins crenate to undulate; petioles to 3 cm long, glabrous to sparingly strigose; pedicels axillary, solitary; bracts linear to 3 cm long, 2 mm wide, apically acute, sparingly sericeous. *Flowers* with the calyx segments linear, to 3.5 cm long, 1.5 mm wide, sericeous and with numerous shorter glandular hairs; corolla white, to 10 cm long, puberulous glandular, the tube funnelform, to 9 cm long, 3 mm broad basally, expanding to 9 mm wide at the mouth, curved to one side, the lobes orbicular, ca. 2 cm in diameter; stamens included, the filaments glabrous, the anthers 5 mm long; ovary pilose, the style hispidulous. *Capsules* not seen.

This species is found in rain forests at lower elevation of western Panama.

BOCAS DEL TORO: Region of Almirante, Buena Vista, *Cooper 216* (NY); *Wedel 423* (MO). COLÓN: 2–3 mi up the Río Guanche, lowland rain forest, ca. 10–20 m, *Kennedy & Foster 2152* (MO).

16. **Ruellia tonduzii** Lindau, Pittier, Primit. Fl. Costaric. 2: 302. 1900. TYPE: Costa Rica, *Tonduz 6778* (B?, not seen).

Erect *herbs* to 35 cm high; stem quadrangular above, the younger portion pilose, glabrous below, the cystoliths prevalent in quadrangular portion. *Leaves* elliptic, 8–12 cm long and 3.0–5.5 cm wide, apically acuminate, basally acute, glabrous except for strigose puberulence along the costa and the veins beneath, the cystoliths numerous but narrow, visible on both the surfaces, margins entire to shallowly crenate; petiole 1–2 cm long. *Inflorescences* a dichasium on a peduncle to 11 cm long, the peduncle quadrangular, slightly winged, puberulous; pedicels to ca. 5 mm long; bracts oblong linear to ca. 10 mm long and 2 mm wide; bractlets linear subulate, ca. 2 mm long. *Flowers* with the calyx and pedicel glabrous to sparingly puberulent, the lobes ca. 3 mm long; corolla mauve, funnelform, to 2.5 cm long, puberulent, the lower half of the tube narrow, 1.5 mm wide, the upper half narrowly campanulate, 7 mm wide at the throat, the lobes suborbiculate, ca. 4 mm wide; stamens included; style 12 mm long, sparingly puberulent. *Capsule* clavate, ca. 15 mm long, 3 mm wide, pointed at the apex and narrowed at the base, glabrous; seeds 8, flat, orbiculate, glabrous, 1.5 mm in diameter.

This species is found on flood plains of rivers and low hills of Pacific coast areas in Panama and Costa Rica.

Corolla and seed measurements were made from Costa Rican specimens: *Dodge & Goerger 9878, 10023* (both F); *Raven 21588* (F).

CHIRIQUÍ: Puerto Armuelles, 0–75 m, *Woodson & Schery* 853, 898 (both MO). COLÓN: Río Guanche, 1–4 km upstream from Portobelo Road, tropical wet plants, 0–100 m, *Gentry 8768* (MO). DARIÉN: Ca. 10 mi S of El Real on Río Pirre, *Duke 5412* (MO).

17. **Ruellia tubiflora** H.B.K. Nov. Gen. Sp. Pl. 2: 241. 1817. TYPE: Colombia (not seen).

17a. **Ruellia tubiflora** var. **tubiflora**

Suffrutescent *herbs* to 1 m tall; younger portions of the stem subquadrangular, glabrous to pilose, densely pilose along the rounded angles. *Leaves* elliptic, to 10–24 cm long and 4–12 cm wide, apically acuminate, basally attenuate, glabrous to pilose at the costa of both surfaces, often with numerous minute, reddish glands or depressions, more numerous beneath, the cystoliths numerous though minute above, the petioles to 1 cm long, the margins entire to slightly undulate. *Inflorescences* in short, terminal spikes with a rachis to ca. 1 cm long; flowers sessile or nearly so; bracts leafy, elliptic, to 5 cm long and 1.5 cm wide, gland dotted, the bracteoles small, subulate, ca. 2 mm long. *Flowers* with the calyx to 4 mm long, gland dotted, segments lanceolate, 1–3 mm long, ca. 1 mm wide, sparingly puberulous; corolla funnelform, curved to one side, red or scarlet, the tube to 5 cm long, ca. 1 cm wide at the mouth, 4 mm wide at the base, puberulous, often gland dotted, the lobes suborbicular, 1.5 cm long, spreading, the limb ca. 3 cm broad; stamens exserted, the anthers saggitate, ca. 3 mm long. *Capsules* clavate, 15 mm long, 5 mm wide, puberulous, gland dotted; seeds 8 or more, orbicular, flattened, 5 mm in diameter, 1 mm thick, sericeous when dry.

This species is found in wet forests or thickets, generally at lower elevations although one specimen is from a cloud forest in Darién above 2,500 ft elevation.

COLÓN: In shade along rocky coast, Garrote, ca. 10 km NE of Portobelo, *D'Arcy 4001* (MO). Santa Rita Ridge, *Dwyer & Gentry 9371* (MO). DARIÉN: Cerro Pirre, 2500–4500 ft, *Duke & Elias 13785* (MO). PANAMÁ: Taboga Island, *Macbride 2802* (US).

17b. **Ruellia tubiflora** var. **tetrasticantha** (Lindau) Leonard, Contr. U.S. Nat. Herb. 31: 91. 1951.—FIG. 28.

R. tetrasticantha Lindau, Pitt. Primit. Fl. Costaric. 2: 300. 1900. TYPE: Costa Rica, *Tonduz 9984* (B?, not seen).

This variety differs from the typical in its white flower, larger leaf size of 15–20 cm long and 6.0–10.5 cm wide, its greater height up to 1.5 m and larger corolla to 8 cm long.

This variety is found in wet forests or thickets generally at lower elevations of Costa Rica, Panama and Colombia (Leonard, 1958).

BOCAS DEL TORO: Region of Almirante, *Cooper 109* (NY). Chiriquicito to 5 mi S along Río Guarumo, *Lewis et al. 2036, 2104* (both MO). Chiriquí Lagoon, Water Valley, *Wedel 1635* (MO). Chiriquí Lagoon, Chiriquí Trail, *Wedel 2172* (MO). Fish Creek Hills, *Wedel 2422* (MO). COCLÉ: Hills N of El Valle de Antón, 800–1000 m, *Allen 2254* (US). 8 mi S of El Valle, *Gentry & Dwyer 3584* (MO). Beyond La Pintada, 400–700 m, *Hunter & Allen 557* (MO). COLÓN: Santa Rita Ridge E of Transisthmian Highway, tropical wet forest, 300–500 m, *Gentry 6549, 6597* (both MO). Santa Rita Ridge Road 4 mi from Transisthmian Highway to Agua Clara weather station, 500 m, *Gentry et al. 8852* (MO). Along road into Santa

FIGURE 28. *Ruellia tubiflora* var. *tetrasticantha* (Lindau) Leonard. Habit (×⅘). [After *Wedel 2172* (MO).]

Rita, E of Agua Clara rain gauge, *Kennedy 2757* (MO). Santa Rita Ridge, *Smith & Smith 3432* (US). Lumber Road about 8 km NE of Santa Rita along ridge, ca. 650 ft, *Wilbur & Weaver 10851* (DUKE). DARIÉN: Cerro de Garagará, Sambu basin, *Pittier 5602* (US).

28. SANCHEZIA

Sanchezia Ruiz & Pavón, Fl. Peruv. Chil. Prodr. 5, *pl. 32.* 1794. TYPE: Not designated.

Erect *herbs* or *shrubs*, mostly glabrous. *Leaves* with numerous cystoliths on both the surfaces, glabrous. *Flowers* solitary or fascicled, usually large and showy, yellow, orange or red, fascicled flowers subtended by bracts which are often large, partly connate and showy; calyx 5-merous; corolla tube cylindric, 5-merous with equal lobes; stamens 2, usually exserted, the anthers 2-celled, mucronulate at the base, puberulous, the staminodes 2. *Capsule* oblong, 6–8 seeded; seeds orbicular.

About 30 species, all native to tropical America and mainly confined to wet forest of the northern Andes comprise this genus. Since they are attractive, they have been widely planted and many have escaped from cultivation.

1. **Sanchezia pennellii** Leonard, J. Wash. Acad. Sci. 16: 488. 1926. TYPE: Colombia, *Pennell 3798* (US).—FIG. 29.

Herbs to 2 m high; stems 4-sided with round angles, glabrous. *Leaves* elliptic to rounded obovate, to 25 cm long and 14 cm wide, acuminate at the apex, the base attenuate, glabrous, the margins crenate. *Inflorescences* in terminal spikes, compact fascicles of 6–8 sessile flowers in the axils of the bracts; bracts to 5 cm long, loosely enclosing the flowers in the connate bases, 2-lobed, 3–3.5 cm wide, the apex acute, red, glabrous, with numerous cystoliths; bractlets to 3.5 cm long and 1 cm wide, elliptic to obovate, acute to obtuse at the apex. *Flowers* with the sepals obovate to 20 mm long, the outer 3 longer, to 5 mm wide, the inner 2 shorter, to 4 mm wide, all obtuse at the apex, glabrous; corolla yellow to orange, tube to 5.5 cm long and to 8 mm wide at the throat, lobes 3 mm wide, obtuse; stamens with the filaments exserted ca. 8 mm beyond the corolla tube, the filaments pilose, the staminodes to 2 cm long; style to 5.5 cm long.

Usually found on banks of streams and along roads and trails in wet forests and common in banana plantations, this species occurs in Colombia and Peru.

DARIÉN: Trail between Pinogana and Yaviza, 15 m, *Allen 269* (MO). Yapé, Río Tuira, *Allen 4300* (MO). Río Pirre, *Croat & Porter 15494* (MO). Road from El Real to Pinogana, *Duke 4897* (MO). Panamerican Highway between Peru and Río Punusa, *Duke & Dwyer 5390* (MO). Río Pirre, old forest 10 mi S of El Real near "Dos Bocas," *Foster 2274* (DUKE). Púcuro, 70 m, *Mori & Gentry 4248* (MO). Forests around Pinogana, *Pittier 6527* (US). SAN BLAS: Hydro Camp Cuadi on Río Cuadi, freshwater Riparian forest, *Duke 15457* (DUKE).

29. STAUROGYNE

Staurogyne Wallich, Pl. Asiat. Rariores 2: 80, *pl. 186.* 1831. TYPE: S. *argenta* Wall.

Herbs or *shrubs*; stems, erect, ascending, or repent, terete or subquadrangular, glabrous or pubescent, hairs often glandular. *Leaves* usually petiolate, entire.

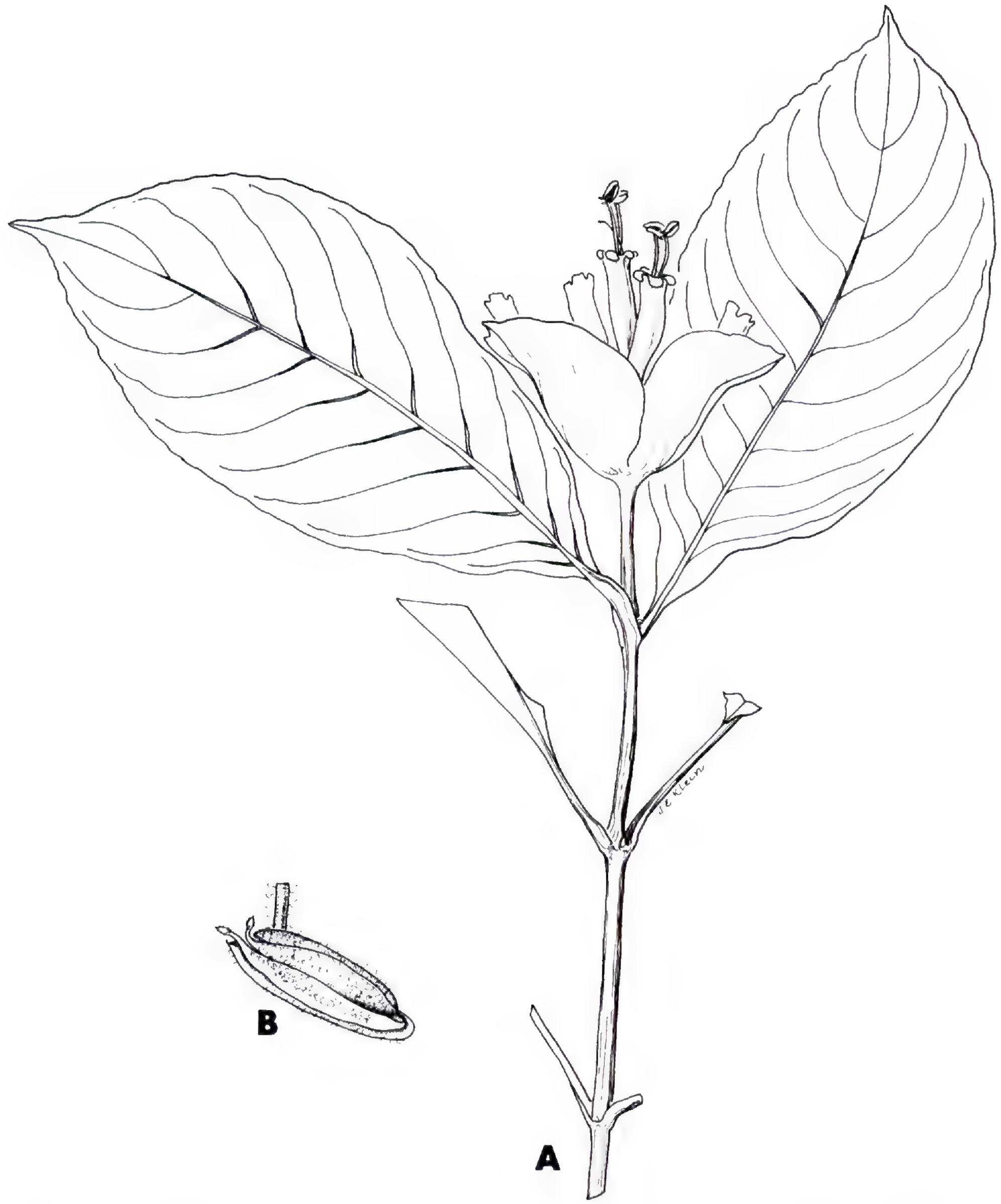

FIGURE 29. *Sanchezia pennellii* Leonard.—A. Habit (×½). [After *Croat & Porter 15494* (MO).]—B. Anther (×3½). [After *Foster & Lowenbach 2274* (MO).]

Flowers sessile or short pedicellate, few to many, in terminal or axillary spikes or racemes; calyx deeply 5-segmented, posterior segment oblong, usually conspicuously longer and broader than the others; corolla usually red, purple or yellow, cylindrical, bilabiate, the upper lip 2-lobed, the lower lip 3-lobed, the lobes rounded; stamens 4, didynamous, usually included, a staminode usually present between the posterior pair, the anthers 2-celled, the sacs subequal, rounded. *Capsules* oblong, obtuse, seeds borne the entire length, retinacula absent; seeds numerous, minute, subglobose.

This is a genus of ca. 80 species distributed in New and Old World tropics, especially Western Malaysia.

1. **Staurogyne agrestis** Leonard, J. Wash. Acad. Sci. 27: 400. *fig. 1.* 1937. TYPE: Panama, *Standley 31936* (US).—FIG. 30.

Herbs to 30 cm tall; stems erect or decumbent, sometimes rooting at the lower nodes, the stems terete, pilose or subtomentose. *Leaves* elliptic to ovate, to 3.5 cm long, 1.5 cm wide, especially acute to obtuse, basally attenuate, sparingly pilose on both the surfaces, the cystoliths absent, the margins serrulate; petioles to 10 mm long, pilose. *Inflorescences* in terminal and lateral spikes to 8 cm long, 1 cm wide, the peduncles pilose, the rachises glandular pilose; bracts elliptic, to 8 mm long, 3 mm wide, apically acute, glandular puberulous, ciliate; bracteoles similar, but narrowly elliptic to 1 mm wide. *Flowers* with 5-merous calyx, the calyx segments linear to 4.5 mm long, ascending hairs to 1 mm long, posterior segment 0.75 mm wide, other segments 0.5 mm wide; corolla light blue, 5.5 mm long, glabrous. *Capsule* oblong, 4 mm long, 1.25 mm wide, glabrous; seeds oval, not flattened, 0.5 mm long, 0.25 mm wide, reddish brown.

This species grows in disturbed sites at lower elevations.

CANAL ZONE: Victoria Fill near Miraflores Locks, *Allen 1702* (MO). Summit Naval Radio Station, *Croat 14248* (MO).

30. TELIOSTACHYA

Teliostachya Nees in Mart., Fl. Bras. 9: 71. 1847. TYPE: *T. cataractae* Nees.

Herbs, ascending or decumbent. *Leaves* ovate to lanceolate with numerous cylindrical cystoliths, the margins entire. *Inflorescences* in dense spikes either terminal or terminal and axillary, the spikes either cylindrical or ovoid; pedicels arranged in whorls of 3–7, the lateral flowers of each whorl subtended by a 1- to 3-nerved bract; 2 bracteoles subtending the lateral flowers, 1-nerved. *Flowers* with the calyx 5-merous, unequal, divided nearly to the base, the posterior lobe much larger than the rest, 3-nerved, the lateral lobes 1-nerved, the anterior lobes longer than the lateral lobes which are 1- or 2-nerved; corolla about as long as the calyx, the tube cylindric, 2-lipped, the upper lips obtuse, emarginate or subentire, the lower lip 3-lobed, the lateral lobes obtuse, the middle lobe emarginate or obtuse; stamens 4, didynamous, the anthers 2-celled, unequal, the lower cell and sometimes both basally apiculate; stigma 2-lobed, the style curved toward the upper lip. *Capsules* oblong, tetrangular, acute; seeds 4, yellow, covered with dense mucilaginous hairs when wet.

This is a genus of about 10 species with only one occurring in Panama. The genus occurs throughout much of tropical America and in West Africa. It closely resembles *Lepidagathis*, an Old World endemic genus. According to Bremekamp (1938), it differs from *Lepidagathis* in that its spike is radially symmetrical and is definitely terminal, the anterior calyx lobes are entirely free, the cells of the anther are unequal, and the pollen grains are entirely free from reticulations. *Lepidagathis* is characterized by a dorsal-ventral, often axillary inflores-

FIGURE 30. *Staurogyne agrestis* Leonard. Habit ($\times 9/10$). [After *Croat 14248* (MO).]

cence, anterior calyx lobes at least partly united at the base, the equal anther cells, and finely reticulate pollen grains.

1. **Teliostachya alopecuroidea** (Vahl) Nees, in Mart., Fl. Bras. 9: 72. 1847.—FIG. 31.

Ruellia alopecuroidea Vahl, Eclog. Amer. 2: 49. 1798. TYPE: West Indies, *Ryan 22196* (C, not seen, photo US).
Lepidagathis alopecuroides (Vahl) R. Br. ex Griseb., Fl. Brit. W. I. 453. 1864.

Herbs to 25 cm high; stems quadrangular, often branched, decumbent or ascending, often rooting at the lower nodes, pilose at the angles. *Leaves* ovate to

FIGURE 31. *Teliostachya alopecuroidea* (Vahl) Nees.—A. Habit (×9/10). [After *Croat* 9244 (MO).]—B. Calyx (×4½). [After *Croat* 7967 (MO).]

ovate elliptic, 2.5–8 cm long and 1.2–3.2 cm wide, apically acute to acuminate, basally attenuate, sparingly pilose above and mainly restricted to the veins beneath, numerous cystoliths more prominently displayed above, entire. *Inflorescences* in dense terminal or axillary spikes to 5 cm long and 1.3 cm wide; flowers in sessile whorls of 3; one bract subtending each whorl and one subtending each lateral flower, obovate oblanceolate, 5 mm long, 1.5 mm wide, apically caudate, basally acute, thin and translucent with the veins prominent, 1- to 3-nerved, transparent when wet, the margins ciliate, the bracteoles subtending the central flower lacking bracts; 2 bracteoles subtending each lateral flower, lanceolate linear, to 5 mm long and 0.4 mm wide, translucent with prominent veins, 1-nerved, ciliate. *Flowers* with the calyx 5-merous, unequal, the anterior pair of segments lanceolate, to 5 mm long, the lateral pair of segments linear, to 3 mm long, the posterior lobe obovate to 6 mm long and 2.6 mm wide, all

the lobes venose and ciliate; corolla white to violet, tubular, to 3.5 mm long and 0.6 mm wide, orbiculate lobes ca. 0.7 mm wide; stamens barely exserted. *Capsules* oblong tetrangular, apically puberulous; seeds 4, yellow lenticular, oval, basally oblique, pilose when dry, hairs densely mucilaginous when wet.

This species occurs in moist areas along trails in rain forests, in thickets and in fields. It ranges through Brazil, British Guiana, Colombia, French Guiana, Peru, Trinidad, and Venezuela and extends into Central America and the West Indies.

CANAL ZONE: Stream bank in rain forest, Fort San Lorenzo, *Durkee et al. 71–125* (MO). Drowned forest of Quebrada Culebra, 70 m, *Steyermark 17214* (MO). BARRO COLORADO ISLAND: *Croat 7319, 7813, 7967, 9244, 13987* (all MO); *Ebinger 283* (MO); *Netting 19* (MO). COCLÉ: La Mesa in cloud forest, *Croat 13352A* (MO). Rain forest at summit of Cerro Pilon above El Valle de Antón, 2700 ft, *Dwyer et al. 4494* (MO). Advanced secondary rain forest, Boca del Toabre at confluence of Río Toabre and Río Coclé del Norte, *Lewis et al. 5486* (MO). Western slopes of Cerro Pajita in the crater of El Valle de Antón and ca. 3 mi N of El Valle, 650 m, *Wilbur et al. 15675* (DUKE). PANAMÁ: Cerro Campana, 850 m, *Maas & Dressler 752* (MO). VERAGUAS: Santa Fé, *Allen 4402* (MO). El Embalsadero, 8 mi W of Santiago, *Tyson 6092* (MO).

31. TETRAMERIUM

Tetramerium Nees in Benth., Bot. Voy. Sulphur 147. 1846, nom. cons. Not *Tetramerium* Gaertner (1805). TYPE: *T. polystachyum* Nees. typ. cons.

Herbs, sometimes suffrutescent; stems erect or declining, much branched, pubescence often arranged in two opposite lines, the old bark often exfoliating. *Leaves* linear to ovate, entire, glabrous or pubescent, sessile or petiolate. *Inflorescences* in terminal, 4-sided spikes; bracts opposite, 4-ranked, conspicuous, often closely imbricate with cuspidate apex; pedicels 2 per bract. *Flowers* with the calyx 4–5-merous, equal, the segments ciliate; corollas funnelform to tubular, the lower lip entire, the upper lip 3-lobed, the lobes about equal; stamens 2, included in the entire lower lobe, the anther cells slightly unequal. *Capsules* clavate, apiculate, 4- or 2-seeded; seeds flattened, papillate or muriculate.

There are approximately 25 species in this genus, which ranges from southern United States to Colombia and Ecuador.

1. **Tetramerium hispidum** Nees in DC., Prodr. 11: 468. 1847. SYNTYPES: Mexico, *Ehrenberg 1072* (B?, not seen); *Allaman* (G-DC, not seen); *Parkinson* (K, not seen); *Linden 191* (K, not seen); *Bejar* (K, not seen).—FIG. 32.

Repent *herbs*, upright portions to ca. 30 cm high; stems terete, pilose when young. *Leaves* ovate to 7 cm long and 4.3 cm wide, apically acute to acuminate, basally rounded to subcordate, sparingly strigose on both the surfaces, numerous cystoliths visible on both the surfaces, entire; petioles to 2.5 cm long, sparingly pilose; some specimens with the leaves also with more numerous small leaves only 2.5 cm long and 1.1 cm wide, and no gradation between these sizes, other specimens with no large leaves. *Inflorescences* terminal to 11 cm long, 1.5 cm wide, the bracts clearly 4-ranked, imbricate, to ca. 13 mm long and 8 mm wide, ovate, apically cuspidate, typically curved outward, basally obtuse, sericeous on

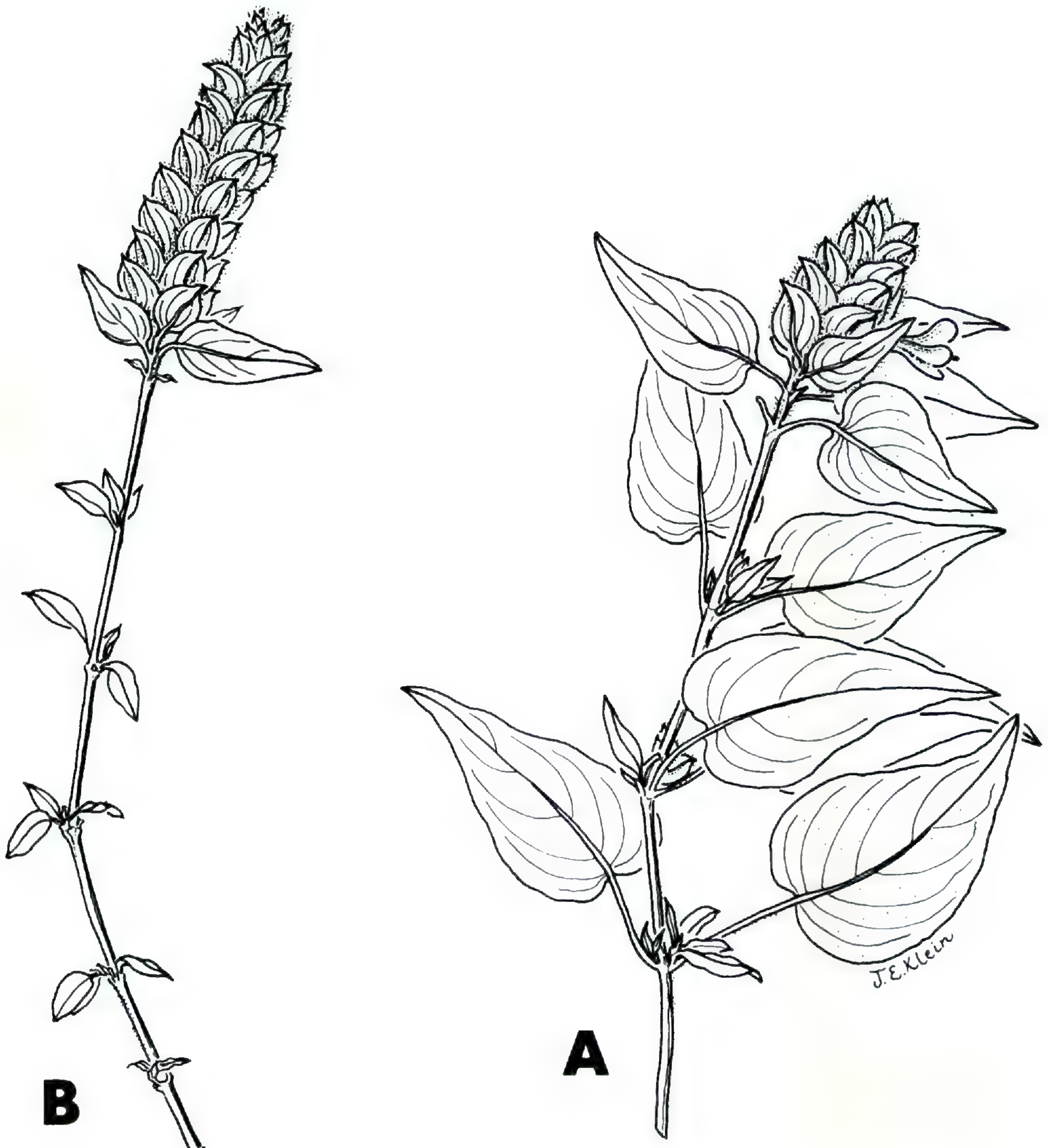

FIGURE 32. *Tetramerium hispidum* Nees.—A. Habit (×9/10). [After *Allen 120* (MO).] —B. Habit (×9/10). [After *Allen 1285* (US).]

both surfaces, ciliate, each bractlet subtending 2 flowers, 2 bracteoles, subulate to ca. 3 mm long, hirsute. *Flowers* with 4-merous calyx, the lobes equal, subulate, to ca. 2.5 mm long, hirsute; corolla white, bilabiate, the tube narrowly funnelform, slightly curved, 6.5 mm long, 1 mm wide at the throat, 0.5 mm wide at the base, the lower lip entire, obovate, 6 mm long and 3 mm wide at widest point, apically rounded, the upper lip 3-lobed, the lobes about equal, obovate, 6 mm long, 2.5 mm wide, apically rounded, all parts of the corolla glabrous; stamens exserted, attached to the base of the lower lip, the filaments to ca. 5 mm long, glabrous,

the cells of anther slightly unequal, light blue. *Capsule* clavate, 5 mm long, 2 mm wide at widest point, 0.5 mm wide at the base, the surface puberulous, containing 2 seeds; seeds suborbiculate, ca. 1.2 mm in diameter, surface papillate.

This species is found along roadsides, trails and other disturbed sites throughout tropical America.

CANAL ZONE: Balboa, *Standley 32111* (US). COCLÉ: Banks of Río Grande, *Burch et al. 1170* (US). Penonomé, 50–1000 ft, *Williams 176* (NY, US). HERRERA: La Avena to outskirts of Pesé, 200 ft, *Burch et al. 1283* (US). PANAMÁ: Taboga Island, *Allen 120* (MO), *1285* (US); *Durkee 71–160* (MO); *Macbride 2789* (US); *Standley 27042, 27866* (both US).

32. THUNBERGIA

Thunbergia Retz., Physiogr. Sälsk. Handl. 1(3): 163. (1780). TYPE: *T. capensis* Retz. nom. cons. not *T. montin*, Kongl. Vetensk. Acad. Handl. 34: 288. *tab. 11.* 1773 (Rubiaceae) nom. rejic.

Herbaceous *vines* or *shrubs*. *Leaves* hastate, rhomboid or ovate. *Flowers* large, peduncled, borne singly in axils or in terminal racemes; bracts 2, foliaceous, large; calyx short, cupuliform, truncate or toothed; corolla 5-merous, funnelform; anthers 4, didynamous, attached near the base of the corolla tube, anthers with an apiculate connective; ovary fleshy, the style apically dilated; ovary basally subtended by a conspicuous fleshy nectary (rounded, entire disc). *Capsule* basally globose extending abruptly into a flattened beak; seeds 2 in each cavity, semiglobose, borne on papilliform funicles.

This genus is chiefly African. Those species found in the neotropics are either under cultivation or have escaped from cultivation.

Thunbergia alata is so thoroughly established in some regions that it appears to be native.

a. Petioles winged; flowers orange or yellow often with a dark purple throat; rarely white ..... 1. *T. alata*
aa. Petioles not winged; flowers not colored as above.
  b. Erect shrub; leaves small, to around 5.5 cm long ..... 2. *T. erecta*
  bb. Vine; leaves to more than 5.5 cm long.
    c. Calyx bearing ca. 12 slender, subulate teeth; corolla tube 2.5 cm long or less, pure white ..... 3. *T. fragrans*
    cc. Calyx annular; corolla tube 3–4 cm long, blue or lavender with yellow throat ..... 4. *T. grandiflora*

1. **Thunbergia alata** Bojar, Sims, Bot. Mag. 52: *pl. 2591.* 1825. TYPE: Grown from seeds procured in Mauritius (not seen).

Herbaceous trailing or climbing *vine* with strigose hairs. *Leaves* deltoid to deltoid ovoid, 4.5–6.5 cm long, acute at the apex, the margins undulate, hastate to cordate at the base, the upper surface sparingly strigose, the lower surface hirsute; petioles winged, to 6.5 cm long. *Inflorescences* with the peduncles mostly longer than the petioles; bracts deltoid ovate with acute tips, hirsute. *Flowers* with the corolla yellow or orange with dark purple eye 1.5–2.0 cm long. *Capsule* depressed globose with a stout, flattened, subulate beak ca. 1 cm long, hirsute.

This species is found in fields, along trails, edges of thickets, gardens, and open waste places in general. It occurs in tropical America, southern and eastern Africa, Hong Kong, Guam, Amboina, the Philippine Islands.

CANAL ZONE: Secondary tropical moist forest, much of it brushy, and roadside at end of "abandoned" road C-29, 6 km E of Gamboa, 160–190 m, *Nee 8971* (MO). COCLÉ: El Valle de Antón, Río Indio trail, 500–700 m, *Hunter & Allen 326* (MO).

2. **Thunbergia erecta** (Benth.) T. Anderson, J. Linn. Soc., Bot. 7: 18. 1864. TYPE: Africa, *Vogel* (not seen).

A *shrub* to 3 m tall; younger stems quadrangular, winged, glabrous. *Leaves* ovate to subrhombic, to 5.5 cm long and 2.8 cm wide, apically attenuate, basally acute, glabrous on both the surfaces, the margins entire to slightly undulate; petioles to ca. 5 mm long, glabrous. *Inflorescences* axillary, the peduncles borne singly, to 2.3 cm long, glabrous; bracts oblong ovate, 1–2 cm long, 5–8 mm wide, apically acute, basally obtuse, glabrous to minutely puberulous at the apex. *Flowers* with the calyx reduced to 10–12 teeth ca. 1 mm long; corolla all white or deep violet with a white or yellowish throat, 3 mm wide at the base, the lobes equal, suborbicular, ca. 1.5 cm across, glabrous; cells of the anthers unequal, the base and the margins of the anther cells puberulous.

This is a cultivated shrub that has escaped, and is naturalized. It is found along roadsides, trails and in gardens.

CANAL ZONE: Hospital grounds, Ancón, 20–80 m, *Pittier 2736* (US). BARRO COLORADO ISLAND: *Croat 6918* (MO). PROVINCE UNKNOWN: Cultivated shrub, *Paul 346* (US).

3. **Thunbergia fragrans** Roxb., Pl. Coromand. 1: 47. 1795. TYPE: Collected at Samulcotah, India, collector and specimen unknown.

T. volubilis Pers., Syn. Pl. 2: 179. 1806. TYPE: India (P-JU, not seen).

Herbaceous climbing or twining *vine*; stems strigose, subquadrangular. *Leaves* ovate to ovate lanceolate, 5–10 cm long, 2.0–5.5 cm wide, chartaceous, the margins undulate, hastate to cordate at the base, the tips acuminate, strigose on both the surfaces; petioles slender, 2–3 cm long. *Inflorescences* with the peduncle borne singly, axillary, to 5 cm; bracts deltoid ovate, 1.5–2.0 cm long, 5–8 mm wide, the tip acute attenuate, the base rounded. *Flowers* with the calyx with 15–20 subulate teeth; corolla white, the tube 2.0–2.5 cm long, the lobes crenate, nearly as long as the tube. *Capsule* depressed globose, tipped by a stout flattened, subulate beak 1.0–1.5 cm long.

Occurring on roadsides, thickets, waste places in general, this species is naturalized after cultivation. It is found in tropical regions throughout most parts of the world.

Leonard (1951) reports that although this species is termed *T. fragrans* there is considerable disagreement about whether the flower is actually fragrant. Some find it so, others only at certain times of the day and still others fail to detect any odor.

BOCAS DEL TORO: Chiriquicito to 5 mi S along Río Guarumo, *Dwyer 2125* (DUKE). Chiriquí Lagoon, Isla Colón, *Wedel 2927* (MO). Old Bank Island, *Wedel 2091* (MO). Changinola, *Lewis et al. 918* (MO). CANAL ZONE: collector unknown (MO). HERRERA: *Ebinger 1039* (MO). LOS SANTOS: Río Tonosí, vicinity of Tonosí, *Lewis et al. 1585* (MO).

4. **Thunbergia grandiflora** Roxb., Hort. Beng. 45. 1914; Fl. Ind. 3: 34. 1832. TYPE: India, collector and specimen unknown.—FIG. 33.

T. cordifolia Nees in DC., Prodr. 11: 35. 1847. TYPE: Assam (K, not seen).

Suffrutescent climbing or twining *vine*; tips of stem quadrangular, young stems strigose. *Leaves* ovate to ovate hastate, 8–16 cm long, 3.0–13.5 cm wide, acuminate at the tip, chartaceous, scabrous on both the surfaces, hastate or rounded at the base, often coarsely toothed or lobed below the middle; petioles 1–5 cm long. *Inflorescences* in axillary or terminal racemes, the bracts irregularly oblong, to 3.5 cm long and 2 cm wide, acuminate, striate nerved, covered with minute dark dots. *Flowers* with the calyx purplish; corolla lavender with yellow center, campanulate, the tube 3.0–4.5 cm long, lobes 3–4 cm long; base of the exterior anther cells of the posterior stamens with rigid sharp curved spurs to 3 mm long, the anterior stamens with only one spur on each. *Capsule* globular, 16 mm in diameter, tipped with a stout, flattened beak about 2 cm long.

This species is distributed in forests, gardens and thickets. It is naturalized in tropical regions of the world.

BOCAS DEL TORO: Chiriquí Lagoon, Old Bank Island, *Wedel 1957, 2163* (both MO). Chiriquí Lagoon, Bastimentos "short cut," *Wedel 2916* (MO). CANAL ZONE: Cultivated in yard in Curundu, *Blum & Tyson 1072* (MO). Forest, Madden Dam, 50 ft, *Lewis et al. 18* (GH, MO). Cultivated, Balboa, *Standley 26988* (US).

33. TRICHANTHERA

Trichanthera H.B.K., Nov. Gen. Sp. Pl. 2: 243. in obs. 1817. TYPE: *Ruellia gigantea*, Humboldt & Bonpland = *Trichanthera gigantea* (Humboldt & Bonpland) Nees.

Shrubs or *trees*. *Leaves* ovate to oblong, entire to undulate, numerous small cystoliths visible on the upper surface. *Inflorescences* in compact terminal panicles (or corymbs). *Flowers* subtended by 2, small, triangular bractlets; calyx 5-merous with the sepals separate, equal and mostly obtuse; corolla regular, 5-lobed, tomentose, campanulate; stamens 4, exserted, didynamous, the anthers ciliate, with 2 equal cells rounded at the base; capsule 4-seeded.

Trichanthera is a genus of two species ranging from Central America to northern South America.

1. **Trichanthera gigantea** (Humb. & Bonpl.) Nees in DC., Prodr. 11: 218. 1847. —FIG. 34.

Ruellia gigantea Humb. & Bonpl., Pl. Aeq. 2: 75, *pl. 102*. 1809. TYPE: Colombia, *Humboldt & Bonpland* (B?, Kew, neither seen).

Shrubs or small *trees* to 17 m; branchlets quadrangular with rounded angles, terminal portions brown tomentose; the lenticles prominent. *Leaves* ovate to

FIGURE 33. *Thunbergia grandiflora* Roxb.—A. Habit (×4/10).—B. Stamens and stigma (×5).—C. Corolla (×3/5). [After *Blum & Tyson 1072* (MO).]

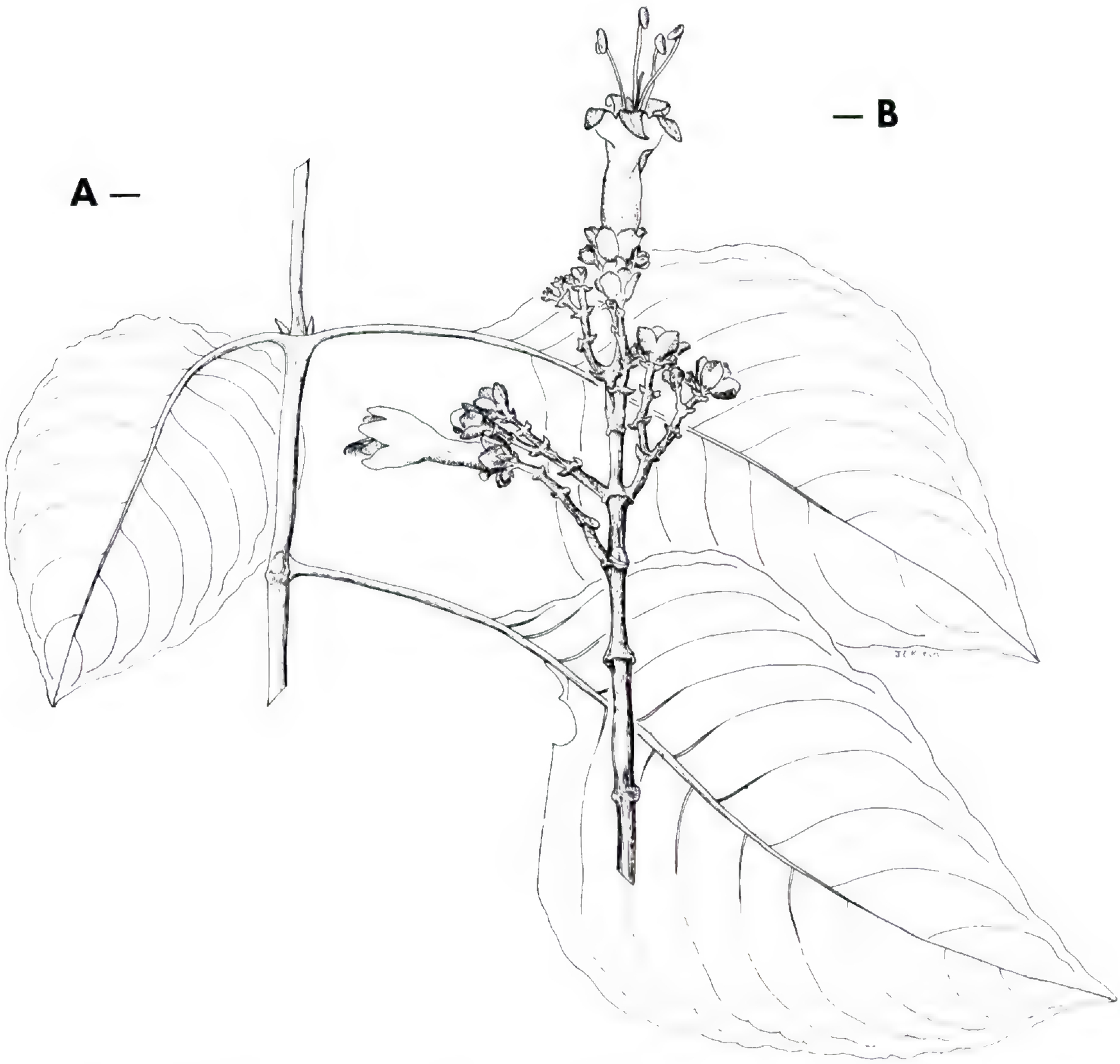

FIGURE 34. *Trichanthera gigantea* (H. & B.) Nees.—A. Habit (×½). [After *Kennedy et al. 2302* (MO).]—B. Inflorescence (×½). [After *Duke 4924* (MO).]

oblong, to 23 cm long and 10 cm wide, apically acuminate or acute, basally obtuse or oblique, the margins entire to slightly undulate, the surfaces glabrous with the costa of the larger leaves sparingly pilose; petioles 1.5 to 6 cm long. *Inflorescences* in terminal compact panicles, tending to be secund, to 15 cm long and 6 cm wide, light brown tomentose. *Flowers* subtended by two triangular bractlets to 3 mm long; sepals 10–12 mm long, tomentose, rounded to acute at the apex; corollas shiny yellow in the throat, brownish red in the expanded portion, 3–4 cm long, glabrous at the throat, silky tomentose above, the tube 1–1.5 cm long, the limb 2–3 cm across; lobes 3–5 cm wide, oblong to oblong ovate; ovary brown tomentose; style 4–5 cm long. *Capsules* to 1.5–2 cm long, obtuse at apex, sericeous.

This species is found along roadsides, in clearings, swampy areas, forests and thickets; it occurs from Costa Rica to Colombia, Venezuela and the Guianas.

CANAL ZONE: Drowned forest of upper Río Pequení between Salamanca Hydrographic Station and Río Boqueron, 70 m, *Allen 17275* (MO). Madden Forest Road 2, *Croat 8957*

(MO). Boyd-Roosevelt Highway, 5 mi W of Sabanita, *Croat 14073* (DUKE, MO). Between Río Pacora and Chepo, *Dwyer 5124* (MO). Chagres River, 3 mi above Gamboa Bridge, *Kennedy et al. 2302* (MO). Along Pipeline Road, 3.5 km NW of Gamboa, 50 m, Nee 10446 (DUKE). BARRO COLORADO ISLAND: *Croat 4632* (MO), *8528* (DUKE, MO); *Dressler 3427* (DUKE, MO); *Foster 1680* (DUKE, MO). COCLÉ: Lower portion of valley and marshes along Río Antón, El Valle, 500 m, *Hunter & Allen 385* (MO). COLÓN: Juan Mina plantation, Río Chagres, 25 m, *Allen 4106* (MO). DARIÉN: *Bristan 124* (MO). 1–5 mi downstream from El Real, *Duke 4924* (MO). Cerro Piriaque, *Duke 8110* (MO). Río Tuira between Río Paya and Río Cube, *Gentry 4354* (DUKE, MO). El Real airport, *Sexton 260, 261* (both MO). Cerro Piriaque at 100–1000 ft, *Tyson 3814* (MO). LOS SANTOS: Tonosí, along Quebrada Ocho Paso, a small tributary of the Río Tonosí, *Stern et al. 1834* (MO). 10 mi N of Tonosí, *Tyson et al. 2948* (MO). PANAMÁ: San José Island, Camp Valley, *Johnston 679* (MO).

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FLORA OF PANAMA[1]

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part IX

FAMILY 182. CUCURBITACEAE

RICHARD P. WUNDERLIN[2, 3]

Monoecious or dioecious, climbing or prostrate, annual or perennial *vines* or *lianas*, rarely *shrubs* or small *trees*; stems usually 5- to 20-sulcate or -angled. *Leaves* alternate, usually petiolate, simple and entire to pinnately or palmately lobed or palmately compound; tendrils lateral, solitary, simple or up to 5-branched, often spirally twisted, rarely absent; estipulate. *Flowers* in axillary, determinate, cymose, racemose, paniculate, or capitulate inflorescences or solitary, unisexual or rarely bisexual, actinomorphic; hypanthium (calyx tube) adnate to the ovary; calyx limb usually (4–)5(–7)-lobate, the lobes imbricate; corolla gamopetalous or polypetalous, inserted on the calyx limb, the petals or the corolla lobes (4–)5(–7), campanulate, rotate, or salverform, valvate. *Staminate flowers* with 5, free, bilocular stamens alternating with the petals (in the primitive condition) or highly modified through cohesion and reduction (in the advanced condition), the anthers straight to conduplicate, extrorse; pistillodium present or absent; nectaries present or absent. *Pistillate flowers* with solitary pistil, the ovary inferior or nearly so (rarely superior), the carpels primitively 5, usually 3, the locules usually 1 with parietal placentation or sometimes 3 with axile placentation, the ovules numerous to solitary, horizontal, pendulous or ascending, anatropous, often surrounded by pulp, the styles 1 or 3, terminal, united or rarely free, with as many branches or stigma lobes as carpels, each branch sometimes bilobate or bifurcate. *Fruit* a berry with a soft or hard pericarp (pepo) or dry, indehiscent or sometimes valvate or porate; seeds often compressed, sometimes winged, the testa multilayered, the cotyledons large, the embryo straight, the endosperm absent.

The Cucurbitaceae is a family of 90–126 genera and 140–1,280 species. The family is widely distributed in both the Old and New World tropics and

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[1] Assisted by National Science Foundation Grant DEB77-04300 (W. C. D'Arcy, principal investigator).

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[3] Dr. Derek Burch, Culebra, Puerto Rico, began the initial investigation of this treatment for which his assistance and contribution is gratefully acknowledged. The author wishes to express sincere thanks to Dr. Hugh C. Cutler, Missouri Botanical Garden, for his assistance with *Cucurbita*, Dr. Thomas B. Croat, Missouri Botanical Garden, for putting at my disposal the manuscript of his Flora of Barro Colorado Island, and Dr. Jennie V. A. Dieterle, University of Michigan, for her advice on various genera.

ANN. MISSOURI BOT. GARD. 65: 285–368. 1978.

0026-6493/78/0285–0368/$08.55/0

subtropics, but extends into the temperate regions of both the northern and southern hemispheres. In Panama approximately 50 species in 23 genera are found. Some of these have been introduced from the Old World either recently or prehistorically.

Economically, the Cucurbitaceae is an important family with several genera commonly cultivated for food: *Cucurbita* (pumpkins and squashes), *Cucumis* (cucumbers and melons), and *Citrullus* (watermelons). Several other genera are also locally used as food: e.g. *Sechium* (cayote), *Sicana* (calabaza), *Momordica* (balsam apple), and *Luffa* (vegetable sponge). Others are grown as ornamentals: e.g. *Cucurbita* (gourds), *Coccinea* (ivy gourd), and *Trichosanthes* (snake gourd). *Lagenaria siceraria* (bottle gourd) has long been used for containers, ladles, musical instruments, food, etc.

The Cucurbitaceae, although an easily recognized family, is difficult taxonomically. It is often difficult or impossible to identify plants to species or sometimes even to genus without flowering (both staminate and pistillate) and fruiting material. Being large vines often with bulky fruits, good herbarium materials are wanting for many species.

Literature:

Cogniaux, A. 1881. Cucurbitaceae *in* A. De Candolle & C. De Candolle, Monographiae Phanerogamarum. Paris 3: 325–1008.

Hutchinson, J. 1967. Cucurbitaceae *in* Genera of Flowering Plants. London 2: 367–419.

Jeffrey, C. 1962. Notes on Cucurbitaceae, including a proposed new classification of the family. Kew Bull. 15: 337–371.

———. 1967. On the classification of the Cucurbitaceae. Kew Bull. 20: 417–426.

Muller, E. G. O. & F. Pax. 1886. Cucurbitaceae *in* A. Engler & K. Prantl, Die Natürlichen Pflanzenfamilien. Leipzig 4(5): 1–39.

Standley, P. C. 1928. Cucurbitaceae *in* Flora of the Panama Canal Zone. Contr. U.S. Natl. Herb. 27: 365–370.

Due to the monoecious and sometimes dioecious nature of the Cucurbitaceae, identification is often difficult when only one type of flower is encountered. Two keys, one based primarily on staminate material and the second based mainly on pistillate or fruiting material, are provided.

KEY 1

a. Stamen filaments free or only slightly connate toward base.
  b. Stamens 5 ..... 8. *Fevillea*
  bb. Stamens other than 5.
    c. Stamen solitary, the anther forming a capitate horizontal ring .. 6. *Cyclanthera*
    cc. Stamens 2 or 3, not disposed as above.
      d. Anthers straight or only slightly curved at one or both ends.
        e. Stamens 3.
          f. Staminate flowers minute, in diffuse panicles ..... 22. *Sicydium*
          ff. Staminate flowers small to moderate in size, solitary, fasciculate, or racemose.
            g. Petals yellow or greenish yellow.
              h. Leaves to 10 cm in diameter; petals erect .. 13. *Melothria*

hh. Leaves over 10 cm in diameter; petals spreading or reflexed ---------- 16. *Posadaea*
gg. Petals white.
i. Calyx cylindrical; tendrils 4-branched -- 15. *Polyclathera*
ii. Calyx cup shaped; tendrils simple or 2-branched ---------- 20. *Selysia*
ee. Stamens 2.
j. Calyx red, the lobes much longer than those of corolla ---------- 10. *Gurania*
jj. Calyx green, the lobes much shorter than those of corolla ---------- 17. *Psiguria*
dd. Anthers conduplicate or flexuous.
k. Petals free to the base.
l. Petals yellow; leaf bases without petiolar glands ---------- 12. *Luffa*
ll. Petals white; leaf bases with petiolar glands ---------- 11. *Lagenaria*
kk. Petals connate at least in the lower part.
m. Leaves pinnatifid or bipinnatifid ---------- 3. *Citrullus*
mm. Leaves entire, lobed, or 3-foliate.
n. Anthers connate.
o. Flowers white or greenish.
p. Petals connate over half their length; fruit fleshy, peponiform ---------- 2. *Cionosicys*
pp. Petals free nearly to the base; fruit a fibrous berry ---------- 1. *Cayaponia*
oo. Flowers yellow or orange.
q. Leaves deeply divided; flowers to 1 cm long; weedy, wild plants ---------- 14. *Momordica*
qq. Leaves entire or shallowly lobed; flowers well over 1 cm long; cultivated plants, rarely escaped ---------- 5. *Cucurbita*
nn. Anthers free.
r. Tendrils simple; calyx lobes erect or spreading ---------- 4. *Cucumis*
rr. Tendrils 3- to 5-branched; calyx lobes reflexed ---------- 21. *Sicana*
aa. Stamen filaments connate.
s. Calyx tube elongate cylindric ---------- 18. *Rytidostylis*
ss. Calyx tube urceolate, campanulate, or rotate.
t. Anthers free, spreading ---------- 19. *Sechium*
tt. Anthers connate.
u. Stamens 3 ---------- 23. *Sicyos*
uu. Stamens 5.
v. Nectaries forming a depressed spherical cushion at the base of the staminal column or pouchlike and sunk in hypanthium base ---------- 9. *Frantzia*
vv. Nectaries not evident ---------- 7. *Elateriopsis*

KEY 2

a. Leaves pinnatifid or bipinnatifid ---------- 3. *Citrullus*
aa. Leaves entire or palmately lobed or divided.
b. Leaves with sessile glands near the base of the blade.
c. Seeds triangular, 3-cornuate at the base ---------- 20. *Selysia*
cc. Seeds ovate or elliptical.
d. Petals connate over half their length; fruit fleshy, peponiform ---------- 2. *Cionosicys*
dd. Petals free nearly to base; fruit a fibrous berry ---------- 1. *Cayaponia*
bb. Leaves eglandular.
e. Fruits with a solitary seed.
f. Pistillate flowers paniculate; fruits globose, less than 1 cm in diameter; spherical ---------- 22. *Sicydium*

ff. Pistillate flowers solitary; fruits ovoid, obovoid, or fusiform, over 1 cm long; seed lenticular.
g. Nectaries forming a depressed spherical cushion at the base of the style or pouchlike and sunk in hypanthium base ..... 9. *Frantzia*
gg. Nectaries not evident ..... 19. *Sechium*
ee. Fruits 2- to many-seeded.
h. Styles distinct; seeds 4–5 cm long ..... 8. *Fevillea*
hh. Styles united; seeds 2 cm long or less.
i. Calyx orange red, lobes longer than corolla ..... 10. *Gurania*
ii. Calyx green or greenish, lobes shorter than corolla.
j. Fruits echinate, tuberculate, or setose.
k. Fruits orange; seeds surrounded by a red aril .. 14. *Momordica*
kk. Fruits greenish; seeds without a red aril.
l. Fruits or pistillate flowers in clusters ..... 23. *Sicyos*
ll. Fruits or pistillate flowers solitary.
m. Calyx tube elongate cylindric ..... 18. *Rytidostylis*
mm. Calyx tube rotate or campanulate.
n. Corolla yellow; tendrils simple; fruits indehiscent ..... 4. *Cucumis*
nn. Corolla white; tendrils branched; fruits explosively or elastically dehiscent ..... 6. *Cyclanthera*
jj. Fruits smooth or roughened, but not echinate (sometimes with a few seta near base).
o. Corolla red; calyx tube elongate cylindrical ..... 17. *Psiguria*
oo. Corolla other than red; calyx tube rotate to campanulate.
p. Corolla yellow or greenish yellow.
q. Calyx lobes reflexed at anthesis.
r. Corolla 2.0–3.5 cm long; fruits fleshy, fusiform, dark red or purple ..... 21. *Sicana*
rr. Corolla 8–9 mm long; fruits with woody pericarp, spherical, greenish yellow ..... 16. *Posadaea*
qq. Calyx lobes erect or spreading.
s. Fruit operculate, interior filled with coarse fibrous mass ..... 12. *Luffa*
ss. Fruit indehiscent, interior pulpy.
t. Corolla less than 1 cm long; fruits less than 6 cm long; wild plants ..... 13. *Melothria*
tt. Corolla over 1 cm long; fruits over 6 cm long; cultivated plants, rarely escaped ..... 5. *Cucurbita*
pp. Corolla white or greenish white.
u. Petioles biglandular at the apex ..... 11. *Lagenaria*
uu. Petioles eglandular.
v. Fruits obliquely ovoid; seeds few, embedded in pulp.
w. Leaves entire or only lobed ..... 7. *Elateriopsis*
ww. Leaves palmately dissected ..... 6. *Cyclanthera*
vv. Fruits ellipsoid or oblong; seeds numerous, in tiers of horizontal ligneous-walled cavities ..... 15. *Polyclathra*

1. CAYAPONIA

Cayaponia Manso, Enum. Subst. Bras. 31. 1836, nom. cons. TYPE: *C. diffusa* Manso.

Arkezostis Raf., N. Fl. N. Amer. 4: 100. 1836. [1838] TYPE: *A. quinqueloba* Raf.
Perianthopodus Manso, Enum. Subst. Bras. 28. 1836. TYPE: *P. espelina* Manso.
Alternasemina Manso, Enum. Subst. Bras. 35: 1836. TYPE: *A. tayvia* Manso.
Druparia Manso, Enum. Subst. Bras. 35. 1836, non Clairville, 1811. TYPE: *D. racemosa* Manso.
Trianosperma (Torr. & Gray) Mart., Syst. Mat. Med. Bras. 79. 1843. TYPE: *T. boykinii* (Torr. & Gray) Roem.
Allagosperma Roem., Fam. Nat. Syn. Monogr. 2: 15, 68. 1846. TYPE: not designated.
Cionandra Griseb., Fl. Brit. W. I. 286. 1860. TYPE: not designated.
Antagonia Griseb., Pl. Lorentz. 96. 1874. TYPE: *A. citrullifolia* Griseb.

Dioecious or monoecious tendriled *vines*; stems 5- to 20-sulcate. *Leaves* petiolate, simple or foliolate; tendrils simple or 2- to 5-branched. *Staminate flowers* in racemes or panicles, or solitary in the axils of the leaves; calyx campanulate or subcylindrical, 5-lobate; corolla campanulate or rotate, 5-lobate; stamens 3, inserted on calyx tube at the base, the filaments free, the anthers longitudinally triplicate, rarely replicate at the apex, connate, one anther unilocular, others bilocular; ovary rudimentary, glandlike, 3-lobed; nectaries present or absent. *Pistillate flowers* usually disposed as the staminate flowers; calyx and corolla usually as in the staminate flowers; ovary ovoid or oblong, 3-carpellate or rarely unicarpellate through abortion, the styles 3, connate, erect, the stigmas 3, forming a peltate, 3-lobate head, the lobes reflexed; nectary disc surrounding the style at the base; staminodia 3, minute, rarely absent. *Fruit* ellipsoid or globose, fleshy, corky, indehiscent; seeds 1–15, erect, ovate or oblong, compressed, the testa smooth or roughened.

Cayaponia consists of 60–70 species mainly of the Neotropics. The genus has not been revised since Cogniaux (1881) and as a result species are often difficult to place. Jeffrey (1971), having found Cogniaux's subdivision into three sections unsound, has realigned the species into two sections: sect. *Cayaponia* and sect. *Trianosperma*. Representatives of both sections occur in Panama.

A single collection of *Cayaponia* from Panama has not been assigned to species. It may represent a species new to Panama or perhaps be undescribed. In view of the scarcity of material, it is unwise to describe it as new.

1. *Pittier 3907* (US). The specimen is trifoliolate, the leaflets 5–8 cm long, 2.5–4.0 cm wide, elliptic, the lateral leaflets oblique at the base and glabrate. The tendrils are unequally 2-branched. An old shattered fruit, apparently moderate in size (ca. 2–3 cm long), glabrous, and 3-seeded, is present. The seeds are 15–16 cm long, 12–14 cm wide, tricornuate at the base and shortly bicornuate at the apex. The label information reads "Along Rio Fato, Province of Colón, in forest or thickets; altitude 10 to 100 meters."

A number of additional species are reported from Colombia and Costa Rica which will perhaps later be found in Panama.

Cayaponia cruegeri (Naud.) Cogn. was reported from Panama by Jeffrey (1971), but the collection cited has been examined and has been assigned to *C. glandulosa*.

Literature:

Jeffrey, C. 1971. Further notes on Cucurbitaceae. II. The tribe Cucurbiteae. Kew Bull. 25: 191–236.

a. Mature leaves 3-foliolate (immature leaves often simple).
  b. Leaves glabrous on both surfaces; fruit reddish orange ..... 3. *C. granatensis*
  bb. Leaves scabrous pubescent above, tomentellous below; fruit dirty yellow ..... 1. *C. buraeavii*
aa. Mature leaves simple.
  c. Flowers sessile or subsessile in axillary clusters, densely pilose ..... 7. *C. sessiliflora*
  cc. Flowers solitary or in pedunculate racemes, pubescent or glabrous.
    d. Hypanthium ca. 4 cm in diameter; fruit 4–6 cm in diameter .. 4. *C. macrocalyx*
    dd. Hypanthium up to 1.5 cm in diameter; fruit to 1.5 cm in diameter.
      e. Corolla ca. 1.5 cm long; fruit 6- to 15-seeded ..... 2. *C. glandulosa*
      ee. Corolla up to 1 cm long; fruit 2- to 3-seeded.
        f. Fruit globose, black (rarely red); tendrils simple, rarely 2-branched ..... 5. *C. micrantha*
        ff. Fruit ellipsoid, orange red; tendrils 2-branched ..... 6. *C. racemosa*

1. **Cayaponia buraeavii** Cogn. in DC., Monogr. Phan. 3: 791. 1881. SYNTYPES: Colombia, *Triana 2993, 5126* (MO, both on same sheet); *Goudot 1* (P, not seen).

C. austin-smithii Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1387. 1938. TYPE: Costa Rica, *Smith A446* (F, holotype, not seen; MO, isotype).

Monoecious *vines*; stems puberulent, glabrescent. Juvenile *leaves* simple or 2- to 3-lobate, the mature leaves 3-foliolate, the middle leaflets elliptic to broadly ovate, the lateral leaflets similar but asymmetrical at the base, the apex acute to caudate, the margin remotely denticulate, subcoriaceous, the upper surface scabrous puberulent, especially on the nerves, minutely white pustulate, the lower surface tomentellous, few sessile, small glands near the base; petiole 4–6 cm long, puberulent; tendrils simple or 2-branched, puberulent or glabrescent. *Staminate flowers* axillary, solitary or few in short racemes, lateral and terminal branches often with reduced leaves and resembling panicles or elongate racemes; rachis and pedicels puberulent; calyx campanulate, 5–8 mm long, the outer surface puberulent, the inner surface sparsely villous, the lobes triangular lanceolate, ca. 2 mm long, puberulent, erect to slightly spreading; corolla white, the lobes broadly lanceolate, ca. 1 cm long, the outer surface tomentellous, the inner surface sparsely villous; filaments ca. 3 mm long, slender, densely short villous above, otherwise glabrous, the anthers complicate, forming an irregular head, ca. 2.5–3.0 mm long and wide; pistillode obsolete, glabrous. *Pistillate* flowers similarly disposed as the staminate flowers; calyx campanulate, 3–4 mm long, puberulent, the lobes linear lanceolate, ca. 2 mm long; corolla lobes linear, otherwise as in the staminate flowers; style 5–6 mm long, the stigma ca. 2 mm long, the ovary subglobose, ca. 5 mm long, puberulent; staminodia ca. 2 mm long, ligulate, villous near the base and at the apex, the cuplike nectary disc surrounding the style at the base. *Fruits* dirty yellow when mature, ovoid, 16–20 mm long, 12–14 mm wide, glabrous, smooth; seeds tan, elliptic, 8–9 mm long, 5–6 mm wide.

Cayaponia buraeavii occurs in Costa Rica, Panama, Colombia, and Venezuela in cloud forests or primary forests at 1,600–2,000 m elevation. In Panama it is known only from the single following collection.

CHIRIQUÍ: Las Nubes, *Croat 26439* (MO).

2. **Cayaponia glandulosa** (Poepp. & Endlich.) Cogn. in DC., Monogr. Phan. 3: 755. 1881.

Bryonia glandulosa Poepp. & Endlich., Nov. Gen. Sp. Pl. 2: 56. 1838. TYPE: Peru, *Poeppig 2211* (LE, W, neither seen).
Trianosperma heterophylla Naud., Ann. Sci. Nat., ser. 4. 16: 144. 1862. SYNTYPES: Colombia, *Triana 3395* (K, P, neither seen; MO, photo of specimen at G), *5126* (P, not seen).
Cayaponia tomentosa Cogn., Bull. Acad. Roy. Belgique, ser. 2. 49: 194. 1880. SYNTYPES: Ecuador, *Andre 3714* (K, not seen); Peru, *Mathews 2046* (E, K, LE, none seen).
C. poeppigii Cogn., Bull. Acad. Roy. Belgique, ser. 2. 49: 195. 1880. TYPE: Peru, *Poeppig 1674* (G, P, W, none seen).
C. ottoniana Cogn. in DC, Monogr. Phan. 3: 755. 1881. TYPE: Venezuela, *Otto 851* (MO, photo of specimen at B, probably destroyed; W, not seen).
C. heterophylla (Naud.) Cogn. in DC., Monogr. Phan. 3: 758. 1881.
Arkezostris glandulosa (Poepp. & Endlich.) Kuntze, Rev. Gen. Pl. 1: 255. 1891.
A. ottoniana (Cogn.) Kuntze, Rev. Gen. Pl. 1: 255. 1891.
A. heterophylla (Naud.) Kuntze, Rev. Gen. Pl. 1: 255. 1891.
A. glandulosa (Poepp. & Endlich.) Kuntze, Rev. Gen. Pl. 1: 255. 1891.
A. poeppigii (Cogn.) Kuntze, Rev. Gen. Pl. 1: 255. 1891.
A. tomentosa (Cogn.) Kuntze, Rev. Gen. Pl. 1: 255. 1891.

Monoecious *vines*; stems pubescent to glabrate. *Leaves* simple, cordate to ovate, entire or 3-lobate, 6–20 cm long and nearly as wide, the apex rounded to acute, the base cuneate to cordate, the margin remotely glandularly denticulate, chartaceous to subcoriaceous, 3-veined, the upper surface white pustulate, both the surfaces pubescent, at least on the veins near the base, the lower surface with sessile glands near the petiole; petiole 2–8 cm long, puberulent; tendrils 1- or 2-branched below the middle. *Staminate flowers* axillary, racemose or paniculate, occasionally solitary, the rachis to 20 cm long, slender, pubescent to glabrate; pedicels 1–5 mm long, stout; calyx campanulate, ca. 1 cm long, obscurely many nerved, pubescent, the lobes broadly rounded, 1–3 mm long; corolla 5-lobate to below the middle, the lobes ovate lanceolate to oblong, ca. 1.5 cm long, greenish white, the outer surface pubescent, the inner surface tomentose, obscurely nerved; filaments ca. 1 cm long, filiform, the anthers complicate, forming an irregular oblong head, ca. 7 mm long; nectaries pouchlike on hypanthium wall toward base, cuplike nectary disc present at base of hypanthium. *Pistillate flowers* disposed as in staminate flowers; calyx and corolla as in staminate flowers; style ca. 1.5 cm long, ovary ellipsoid, puberulent to glabrate, 4–6 mm long; nectaries as in the staminate flower, a cuplike nectary disc surrounding style at base; staminodia minute. *Fruits* purplish black, ellipsoid to subglobose, ca. 2 cm long, ca. 1.5 cm in diameter, the surface smooth, glabrous; seeds 6–15, obovate, ca. 6 mm long, ca. 4 mm wide, brown and white mottled, the testa smooth.

Cayaponia glandulosa is a common lowland, tropical, moist forest species known from Colombia, Venezuela, Peru, Ecuador, Bolivia, and Panama. Highly polymorphic, it is easily confused with the more common *C. racemosa* in the absence of flowers or fruits.

BOCAS DEL TORO: Santa Catalina, *Blackwell et al. 2726* (MO). Changuinola Valley, *Dunlap 35* (F). Chiriquí Lagoon, Changuinola River, *Wedel 2604* (F, GH, MO, US). CANAL ZONE: Military Road K-9, *Ebinger 532* (MO, US). Around Gamboa, *Pittier 3696* (F, NY, US). Aqua Clara, on the Trinidad River, *Pittier 4038* (NY, US). Cuatro Calles Hills, near Matachin, *Pittier 4040* (US). Frijoles, *Standley 31484* (US). Darién Station, *Standley 31519*

(US). BARRO COLORADO ISLAND: *Bailey & Bailey 577* (F, GH); *Kenoyer 573* (US); *Shattuck 73* (F, MO), *90* (F, GH, MO); *Standley 41133* (US); *Starry 162* (F); *Wetmore & Woodworth 74* (F). CHIRIQUÍ: Las Nubes, 5.5 km NW of Río Chiriquí Viejo, W of Cerro Punta, *Busey 683* (F, MO). San Bartolo Arriba W of Puerto Armuelles, *Croat 26701* (MO). Bajo Chorro, *Davidson 372* (F, MO). Puerto Armuello, *Davidson 1199* (F). Monte Verde, 2.5 km W of Puerto Armuelles, *Liesner 66* (MO, US). Quebrada Tuco, 9 mi S of Puerto Armuelles, *Liesner 159* (MO). Boquete, *Terry 1280* (F). Río Chiriquí to Remedios, *Woodson et al. 1193* (F, GH, MO, NY). COCLÉ: Road from El Valle de Antón to La Mesa, *Dwyer et al. 604* (MO). COLÓN: San Juan near Cement Plant Lake, *Blum & Tyson 536* (MO). Along Río Guanche 3–5 mi inland, *Croat 26220* (MO). Along Río Fató, *Pittier 3868* (US). Along the Río Sirri, Trinidad Basin, *Pittier 4038* (US). DARIÉN: Río Tuqueza below Quebrada Venado, *Bristan 1036* (USF). Río Ucurganti, *Bristan 1144* (MO). Airstrip at Cana gold mine, *Croat 37965* (MO). Río Pirre, *Duke 4968* (GH, MO). Road from El Real to Pinogama, *Duke 5137* (GH, MO). Trail between Paya and Payita, *Stern et al. 375* (GH, MO, US). Trail between Caná and Boca de Cupe, *Stern et al. 620* (GH, MO, US). Campamento Buena Vista, Río Chucunaque above Río Tuquesa, *Stern et al. 861* (GH, MO, US). Periaque Camp at river, *Tyson et al. 4740* (FSU, MO). PANAMÁ: Panamerican Highway near Jenine, Río Cañita, *Duke 3817* (GH, MO). Piria-Cañasas trail near Piria, *Duke 14318* (MO, NY). Tocumen, *Dwyer 4033* (FSU, MO), *5129* (MO). N of El Llano, *Gentry 5564* (F, MO, NY). Near Tapia River, Juan Diaz region, *Maxon & Harvey 6759* (GH, US). Marsh area 2 mi S of Tocumen Airport, *Tyson & Clewell 5887* (DUKE).

3. **Cayaponia granatensis** Cogn. in DC., Monogr. Phan. 3: 794. 1881. LECTOTYPE: Colombia, *Karsten s.n.* (W, not seen).—FIG. 1.

Arkezostis granatensis (Cogn.) Kuntze, Rev. Gen. Pl. 1: 255. 1891.

Dioecious *vines*; stems glabrous. Juvenile *leaves* simple, mature 3-lobate or 3-foliolate, the blade of the juvenile leaves elliptic to narrowly ovate, 10–20 cm long, 5–10 cm wide, the apex long acuminate, the base rounded to cuneate, 1-nerved, the mature leaves broadly ovate, 14–25 cm long and wide, the apex of the lobes or the leaflets caudate, the base truncate to cordate, 3-nerved, all leaves with the margins entire and minutely denticulate, chartaceous to coriaceous, both the surfaces glabrous, eglandular or with a few small, sessile glands near the petiole; petiole 2.5–9.0 cm long, stout, glabrous; tendrils 3-branched near the base. *Staminate flowers* in short, axillary, fasciculate racemes, the rachis 1–2 cm long, puberulent; pedicels 1–3 mm long, stout; calyx campanulate, ca. 2 mm long; corolla white, the lobes ovate lanceolate, 1.0–1.5 cm long, the outer surface scabrous pubescent, crisp villous on the margins, the inner surface crisp villous; filaments 5–7 mm long, slender, the anthers complicate, forming an irregular head 8–10 mm long; nectaries pouchlike on hypanthium wall near base, a cuplike nectary disc present at the base of the hypanthium. *Pistillate flowers* similarly disposed as the staminate flowers; mature flowers not seen. *Fruits* reddish orange, drying orange, globose, ca. 1.5 cm in diameter, obscurely alveolate, glabrous; seeds 3, broadly elliptic to suborbicular, 12–15 mm long, 7–12 mm wide, light tan, testa smooth or nearly so.

Cayaponia granatensis is a lowland, tropical, moist forest species known from Brazil, Colombia, Venezuela, Peru, and Panama.

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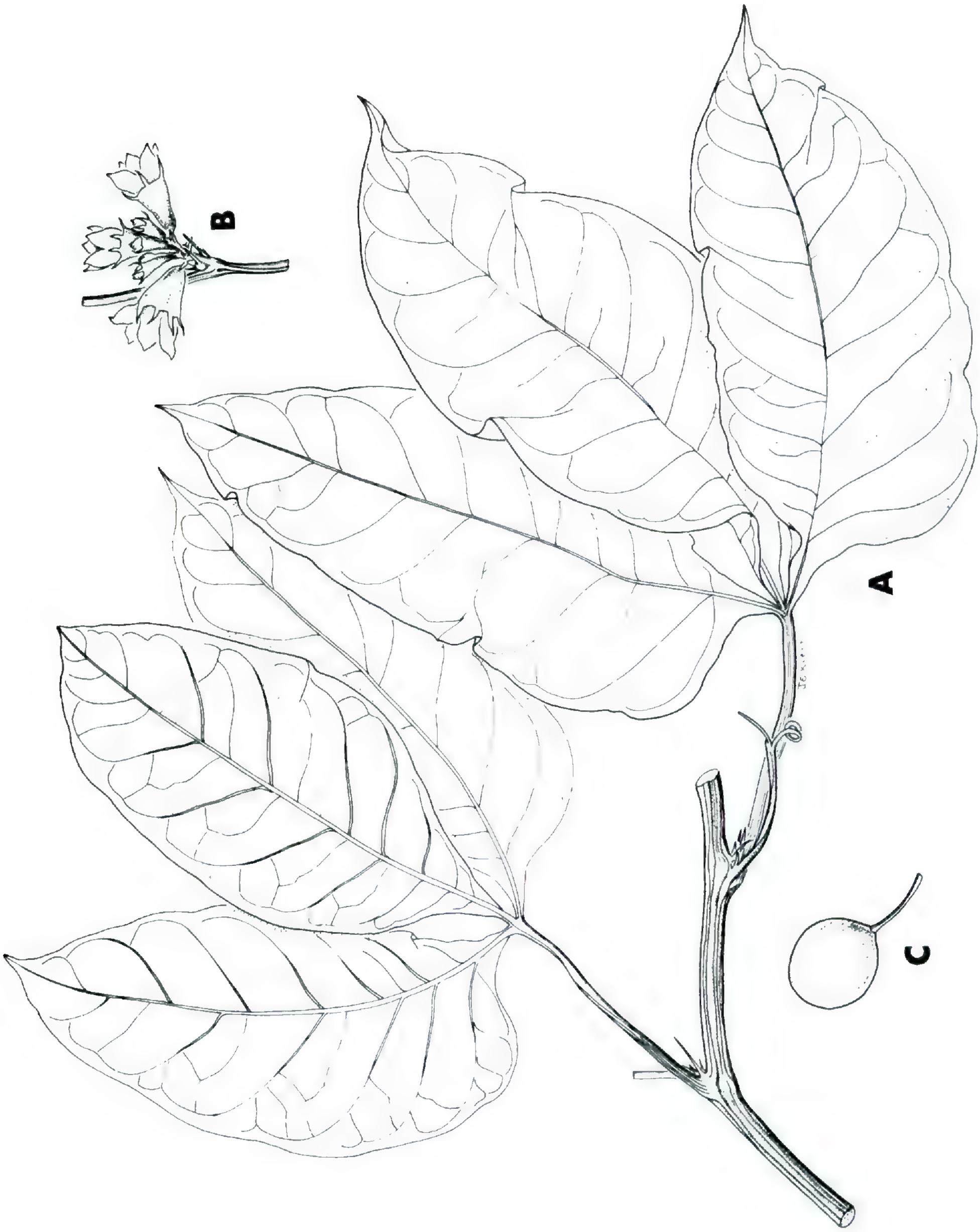
FIGURE 1. *Cayaponia*—A. B. *C. granatensis* Cogn.—A. Habit (×⅖). [After *Liesner 1282*].—B. Inflorescence (×⅖). [After *Allen 4389*].—C. *C. micrantha* Cogn. (×⅘). [After *Croat 12990*].


A
B
C

BARRO COLORADO ISLAND: *Croat 11640, 11668, 13931, 15008, 16215* (all MO); *Foster 2208* (DUKE); *Stoutamire 2114* (MICH); *Wetmore & Woodworth 70* (F), *907* (GH). DARIÉN: Gold mine along Río Caná, SW of Río Pirre, *Croat 27314* (MO). PANAMÁ: Cerro Jefe, *Dwyer et al. 7243* (MO). SAN BLAS: Road from El Llano to Cartí-Tupile, *Liesner 1282* (MO). VERAGUAS: Slopes of Cerro Tuté, vicinity of Santa Fé, *Allen 4389* (MO).

4. **Cayaponia macrocalyx** Harms, Notizbl. Bot. Gart. Berlin-Dahlem 9: 994. 1926. TYPE: Peru, *Tessmann 4445* (B, not seen, probably destroyed, photo MO).

Monoecious *vines*; stems glabrous. *Leaves* simple, suborbicular, deeply 3-lobate, the apex acuminate, the base cordate, the margin remotely and minutely denticulate, chartaceous, the upper surface minutely white pustulate, otherwise glabrous, sessile glands present near the base; petiole 3–5 cm long, slender, glabrous; tendrils simple or 2-branched. *Staminate flowers* solitary in the axils of the leaves; calyx urceolate, ca. 2–4 cm in diameter, glabrous, the lobes acuminate, 1–3 mm long; corolla greenish yellow, the inner surface yellowish orange, the lobes broadly lanceolate to ovate, ca. 3 cm long, both the surfaces pubescent; filaments slender, the anthers complicate, forming an irregular oblong head; nectaries pouchlike on the hypanthium wall near base, cuplike nectary disc present at the base of the hypanthium. *Pistillate flowers* disposed as in the staminate flowers; calyx and corolla as in the staminate flowers; styles ca. 2 cm long, the ovary globose, ca. 2 cm long, glabrate. *Fruits* purplish green, globose, 4–6 cm in diameter, glabrous; seeds 3, ovoid, basally tricornuate, 2.0–2.5 cm long, 1.5–1.7 cm wide, light brown.

Cayaponia macrocalyx is an uncommon and poorly known species of lowland, tropical, moist forests and thickets, usually occurring in river valleys. It occurs in Peru, Ecuador, Colombia, Venezuela, and Panama.

COLÓN: Al este de zona montañosa de Santa Rita, *Correa & Dressler 687* (MO). VERAGUAS: Banks of first river on road between Alto Piedra School and Río Calovebora, 1.8 mi beyond school, *Croat & Folsom 34107* (MO).

5. **Cayaponia micrantha** Cogn., Bull. Acad. Roy. Belgique, ser. 2. 49: 196. 1880. TYPE: Colombia, *Andre 2864* (K, not seen).

Arkezostis micrantha (Cogn.) Kuntze, Rev. Gen. Pl. 1: 255. 1891.

Monoecious *vines*; stems pilose, glabrescent. *Leaves* simple; lanceolate to ovate, obscurely to deeply 3-lobate, if deeply lobate, the lateral lobes half the size of the middle, 3–8 cm long, 1.5–8.0 cm wide, the apex acuminate, the base truncate to deeply cordate, the margin denticulate, chartaceous, the upper surface minutely white pustulate, scabrous pubescent, the lower surface pubescent, sessile glands near the base; petiole 7–20 mm long, pubescent; tendrils simple, rarely 2-branched. *Staminate flowers* solitary in the axils of the leaves; calyx campanulate, 2–3 mm long, puberulent, the lobes triangular lanceolate, ca. 1 mm long; corolla white, the lobes lanceolate, 3–4 mm long, the outer surface pubescent, the inner surface sparsely glandular pubescent; filaments slender, the anthers complicate, forming an irregular, oblong head; nectaries pouchlike on the hypanthium wall near base, cuplike nectary disc present at the base of

the hypanthium. *Pistillate flowers* disposed as in staminate flowers; calyx and corolla as in the staminate flowers; styles ca. 3 mm long, the ovary globose, 3–5 mm long, glabrate; nectaries as in the staminate flowers, a cuplike nectary disc surrounding the style column at the base; staminodia minute, slender. *Fruits* black, globose, ca. 1 cm in diameter, the surface puncticulate, glabrous; seeds 2–3, ovoid, ca. 7 mm long, ca. 5 mm wide, brown mottled, the testa puncticulate.

This species ranges from Panama to Ecuador, occuring in forests and thickets. In Panama, it has been collected only in the Canal Zone and Panama Province, but is to be expected in Darien. Standley (1928) reported this species as common on the Pacific slopes and stated that it has bright red fruits at maturity. *Cayaponia micrantha* usually has black fruits, although var. *coccinea* with red fruits has been described. Jeffrey (1971) states that the red fruited variety is known only from the type collection made in Colombia and that it may represent *C. triangularis* (Cogn.) Cogn. The red fruited Panama specimens appear identical to the black-fruited specimens in all other respects and it is possible that *C. micrantha* is synonymous with *C. triangularis*. This point needs further investigation.

CANAL ZONE: Juan Mina, *Bartlett & Lasser 16526, 16526A* (both MICH). Cocoli Road, *Burch et al. 1398* (GH, MO, US). Road C-21 near Police Lodge, *Croat 12990* (DUKE, F, MO, NY, USF). Gaillard Highway between Paraiso and Summit, *Croat 13257* (MO, USF). Fort Sherman, *Dwyer 7202* (MO, USF). Juan Franco, *Heriberto 269* (GH, NY, US). Sabanas N of Panama City, *Paul 576* (US). Bella Vista, *Piper 5363* (US). Cerro Gordo, near Culebra, *Standley 26043* (MO, US). Along the Old Las Cruces Trail between Fort Clayton and Corozal, *Standley 29014* (US). COLÓN: Ca. 3 km from Pelona, *Carrasquilla et al. 380* (MO). PANAMÁ: Near Tapia River, Juan Diaz region, *Maxon & Harvey 6712* (US). Las Sabanas, *Standley 25871, 25931* (both US). Near the Big Swamp E of the Río Tocumen, *Standley 26528* (US). Río Tapia, *Standley 28220* (US). Near Matías Hernández, *Standley 28883* (US). Río Tocumen, *Standley 29386, 29485* (both US).

6. **Cayaponia racemosa** (Mill.) Cogn. in DC., Monogr. Phan. 3: 768. 1881.

Bryonia racemosa Mill., Gard. Dict. ed. 8. 1768. Based on *Bryonia racemosa foliis ficulneis* Plumier, Nov. Pl. Amer. Gen. Cat. Sp.: 3. 1703; Desc. Pl. Amer.: 83, *tab.* 97. 1693. TYPE: Haiti, *Plumier* (P, not seen).
B. latebrosa Aiton, Hortus Kew. 3: 38. 1789. TYPE: Cultivated at Kew (BM, holotype, not seen).
Cayaponia latebrosa (Aiton) Cogn. in DC., Monogr. Phan. 3: 776. 1881.
Arkezostis latebrosa (Aiton) Kuntze, Rev. Gen. Pl. 1: 255. 1891.
A. racemosa (Mill.) Kuntze, Rev. Gen. Pl. 1: 255. 1891.

Monoecious *vines*; stems puberulent to glabrate. *Leaves* simple, blade elliptic to cordate in outline, entire or 3-lobate to palmately divided, 5–15(–20) cm long, 3–15(–20) cm wide, the apex rounded to acute, the base cuneate to cordate, the margin remotely glandular denticulate, chartaceous to subcoriaceous, the upper surface white pustulate, scabrous pubescent, at least on the nerves near the base, the lower surface scabrous pubescent, sessile glands present near the base; petiole 1.5–6.0 cm long, slender, pubescent to glabrate; tendrils 2-branched below the middle. *Staminate flowers* axillary, racemose or paniculate, occasionally solitary, the rachis to 15 cm long, slender, pubescent to glabrate; pedicels 3–6 mm long, slender; calyx campanulate, ca. 5 mm long, obscurely nerved, pubescent, the lobes broadly triangular, ca. 1 mm long; corolla yellowish white or greenish

white, the lobes ovate lanceolate, ca. 1 cm long, the outer surface pubescent, the inner surface tomentose, obscurely nerved; filaments ca. 4 mm long, slender, the anthers complicate, forming an irregular oblong head ca. 3 mm long; nectaries pouchlike on hypanthium wall near the base, a cuplike nectary disc present near the base of the hypanthium. *Pistillate flowers* disposed as in the staminate flowers; calyx and corolla as in staminate flowers; style ca. 6 mm long, the ovary ellipsoid, puberulent to glabrate, 4–6 mm long; nectaries as in the staminate flowers, cuplike nectary disc surrounding the base of the style column; staminodia absent. *Fruits* orange to red, ellipsoid to ovoid, 1.3–2.0 cm long, 0.8–1.0 cm in diameter, the surface smooth, glabrous; seeds 2–3, ellipsoid, ca. 8 mm long, ca. 5 mm wide, orangish brown, the testa roughened.

Cayaponia racemosa is a frequent and widespread plant of lowland, tropical, moist forests and thickets, usually in coastal river valleys. It occurs in Mexico, Central America, Panama, the West Indies, and the northern part of South America. *Cayaponia racemosa* is said to be poisonous, especially to cattle (Standley, 1928). In El Salvador, the species is known locally as "sandia de culebra," "hierba coral," "camara," and "Taranta."

BOCAS DEL TORO: From Guaymi garden on Río San Pedro, *Gordon 4* (MO). CANAL ZONE: Río Chilibre, tributary of Chagres River between Juan Mina and Madden Dam, *Bartlett & Lasser 16420A* (MICH). Fort San Lorenzo, *Ebinger 471* (F, MO, US). 2 mi N of Paraíso on Balboa Highway, *Lazor & Blum 5313* (FSU). Chiva-Chiva Trail, Red Tank to Pueblo Nuevo, *Piper 5739* (NY, US). Barro Colorado Island, *Starry 162* (MO). Howard Air Force Base near Red Devil Drop Zone, *Tyson 1858* (MO). Ancon Hill, *Williams 35* (NY). COCLÉ: Banks of Río Grande, *Burch et al. 1169* (GH, MO, US). 1–5 mi S of Antón, on old road leading to coast, *Tyson & Blum 2573* (FSU, MO). CHIRIQUÍ: Vicinity of Boquete, *Lewis et al. 386* (MO); *Terry 1280* (GH, MO, US). COLÓN: Along Río Iguanitos, *Elias & Kirkbride 1628* (DUKE, MO). Achiote, *Tyson et al. 4506* (FSU, MO). DARIÉN: Quebrada Bidoto (Peccary Creek) off Río Areti, *Duke 13597* (MO). HERRERA: Vicinity of Chitré, *Allen 1103* (MO, US). PANAMÁ: Near beach at Nueva Gorgona, *Duke 4511* (MO), *4512* (GH, MO, US). Tocumen, *Dwyer 4402* (FSU). San José Island, *Johnston 843, 844* (both GH), *1401* (GH, MO, US). Las Sabanas, *Standley 25918* (MO, US). VERAGUAS: El Embalsadero, 8 mi W of Santiago, *Tyson 6084* (FSU, MO).

6. **Cayaponia sessiliflora** Wunderlin, Phytologia 38: 220. 1978. TYPE: Ecuador, *Dodson 6159* (SEL, holotype; MO, USF, isotypes).

Vines; stem deeply 5-sulcate, puberulent, often also sparsely pilose, glabrescent. *Leaves* elliptic ovate, 9–21 cm long, 6–11 cm wide, the apex acuminate, the base truncate, the margin remotely denticulate, subcoriaceous, the upper surface sparsely pubescent on the primary nerves, otherwise glabrous, finely reticulate nerved, slightly bullate, the lower surface pubescent, densely so on the nerves, conspicuously reticulate nerved; petiole 0.8–2.5 cm long, pubescent, often also sparsely pilose; tendrils slender, simple or unequally 2-branched, pubescent, often also sparsely pilose. *Staminate flowers* axillary in sessile or subsessile, few-flowered clusters; calyx campanulate, ca. 3 mm long, the outer surface densely brown pilose, the inner surface pilose near the top, otherwise glabrous, the lobes subulate, ca. 3 mm long, densely brown pilose, spreading or reflexed; corolla greenish, triangular, 0.5 mm long, the outer surface pilose, the inner surface densely pubescent; filaments stout, ca. 0.5 mm long, pubescent at

the base, the anthers complicate, forming an irregular head 2.5–3.0 mm long and nearly as wide; pistillode obsolete. *Pistillate flowers* not seen. *Fruits* yellowish orange, globose, ca. 3 cm in diameter, sparsely brown pilose, the peduncle ca. 5 mm long; seeds not seen.

Although sterile, the single Panamanian collection appears to be this species. *Cayaponia sessiliflora* is otherwise known only from the type and one additional collection, both from Ecuador. The species occurs in mature forests at 150–250 m elevation.

CANAL ZONE: Barro Colorado Island, *Montgomery 96* (MICH, MO).

2. CIONOSICYS

Cionosicys Griseb., Fl. Brit. W. I. 288. 1860. TYPE: *C. pomiformis* (Macfadyen) Griseb.

Monoecious, tendriled herbaceous or suffrutescent *vines*; stems 5-sulcate. *Leaves* petiolate, entire, angulate or palmately 3- to 5-lobate; tendrils simple or 2-branched. *Staminate flowers* solitary or few in the axils of the leaves; calyx campanulate, 5-lobate; corolla campanulate, 5-lobate almost to the base; stamens 3, the filaments free, the anthers connate, theca replicate, one unithecous, others bithecous. *Pistillate flowers* solitary in the axils of the leaves; calyx and corolla as in the staminate flowers, but smaller; ovary ovoid, the stigmas 3, forming a peltate, 3-lobed head. *Fruits* globose, peponiform, indehiscent; seeds numerous, horizontal, ovate or oblong, subcompressed, the testa smooth.

Cionosicys is a genus of 3 species of Middle America and the Caribbean with one species in Panama.

Literature:

Jeffrey, C. 1971. Further notes on Cucurbitaceae. II. The tribe Cucurbiteae. Kew Bull. 25: 191–236.

1. **Cionosicys macranthus** (Pittier) C. Jeffrey, Kew Bull. 25: 200. 1971.—FIG. 2.

Cayaponia macranthera Pittier, Contr. U.S. Natl. Herb. 13: 118. 1910. TYPE: Costa Rica, *Tonduz 12840* (US, holotype).
C. microdonta Blake, Contr. U.S. Natl. Herb. 24: 27. 1922. TYPE: Guatemala, *Blake 7730* (US, holotype).

Large *vines*; stems glabrate. *Leaves* cordate-ovate in outline, 7–12 cm long, nearly as wide; deeply 3- to 5-lobate, sometimes unlobed, the apex obtuse to acuminate, the blade somewhat decurrent on petiole, the margin irregularly and often obscurely denticulate, firm to chartaceous, scabrous to glabrate; petiole 1–3(–4) cm long; tendrils simple or 2-branched. *Staminate flowers* axillary, usually solitary; peduncle 3–7 cm long, slender; calyx tubular campanulate, 10–14 mm long, puberulent, the lobes triangular, 2–4 mm long, green; corolla white or cream-colored, lobes oblong-ovate, 1.5–2.0 cm long, papillose-pubescent on both surfaces, villous toward base within; androecial head ca. 1 cm long. *Pistillate flowers* solitary in the same axils as staminate; peduncle 1–2 cm long; calyx and

FIGURE 2. *Cionosicys macranthus* (Pittier) Jeffrey. Habit (×½). [After *Gentle 1420*—Belize].

corolla as in staminate, but smaller; ovary ovoid, 6–8 mm long, puberulent. *Fruits* green with cream or light green stripes, 3–5 cm in diameter, globose, peponiform, glabrous, smooth; seeds dark brown, elliptic-ovate, subcompressed, ca. 1 cm long.

This species occurs in moist forest and open thickets often along streams from Mexico to Panama. The following single collection has been seen from Panama.

BOCAS DEL TORO: Talamanca Valley, *Carleton 112* (US).

3. CITRULLUS

Citrullus Schrad. ex Ecklon & Zeyh., Enum. Pl. Afric. Austral. 279. 1834, nom. cons. TYPE: *C. vulgaris* Schrad.

Colocynthis Miller, Gard. Dict. abr. ed. 4. 1754. TYPE: not designated.

Monoecious, tendriled *vines*; stems creeping, 5- to 10-sulcate. *Leaves* petiolate, deeply pinnatifid, the lobes often further divided; tendrils 2- to 5-branched, rarely spinescent. *Staminate flowers* solitary or rarely fasciculate; calyx broadly campanulate, 5-lobate; corolla rotate or broadly campanulate, deeply 5-lobate; stamens 3, inserted on the calyx tube at the base, the filaments free, short, the anthers free or slightly connate, flexuous, 1 anther unilocular, others bilocular; pistillodium glanduliform. *Pistillate flowers* disposed similarly to the staminate flowers; calyx and corolla as in the staminate flowers; ovary ovoid, 3-carpellate, the styles 3, connate, the stigmas 3, reniform, somewhat bilobate; staminodia 3, short, setiform or ligulate. *Fruits* globose or oblong, large, fleshy or dry, indehiscent; seeds numerous, horizontal, oblong, compressed, marginate or emarginate.

Citrullus is an Old World genus of 3 or 4 species with many variants and cultivars. It is widely distributed in the tropics and warm temperate regions of the world, and it is often spontaneous after cultivation. The following single species is known from Panama.

Literature:

Cogniaux, A. & H. Harms. 1924. Cucurbitaceae: Cucurbiteae—Cucumerinae in A. Engler. Das Pflanzenreich 88 (IV, Fam. 272, II): 1–246.

1. **Citrullus lanatus**[4] (Thunb.) Mats. & Nakai, Cat. Sem. Spor. Hort. Bot. Univ. Imp. Tokyo 30, no. 854. 1916.—FIG. 3.

Cucurbita citrullus L., Sp. Pl. 1010. 1753. TYPE: without locality (LINN 1151.5, microfiche).
Momordica lanata Thunb., Fl. Cap. 36. 1807. TYPE: not known.
Citrullus vulgaris Schrad. ex Ecklon & Zeyh., Enum. Pl. Afric. Austral. 279. 1834. TYPE: not known.
C. edulis Spach, Hist. Nat. Vég. Pahn. 5: 214. 1838. TYPE: not known.
Colocynthis citrullus (L.) Kuntze, Rev. Gen. Pl. 1: 256. 1891.

Annual, creeping, *vines*; stems lanate when young, later glabrescent. *Leaves* triangular ovate, 8–20 cm long, 5–15 cm wide, pinnatifid or bipinnatifid, the lobes broad, the sinuses rounded, the apex of the lobes rounded or acute, the base cordate, 3-veined, the margin undulate or irregularly toothed, pale green, chartaceous, the upper surface sparsely lanate on the veins, glaucous, minutely pustulate dotted, the lower surface somewhat lanate, especially on the veins; petioles villous or lanate, 3–8 cm long, striate; tendrils villous or lanate, 2- to 5-branched. *Staminate flowers* axillary, usually solitary, moderate in size; peduncles 2–4 cm long, villous or lanate; calyx broadly campanulate, ca. 1 cm long, green, villous, the lobes linear lanceolate, subequalling the tube; corolla campanulate, 2.5–3.0 cm long, the lobes ovate oblong, obtuse, yellow, the outer surface villous, the inner surface papillose, 5-nerved; filaments 2–3 mm long, stout, glabrate, slightly

[4] See Cogniaux and Harms (1924: 103–104) for additional synonyms.

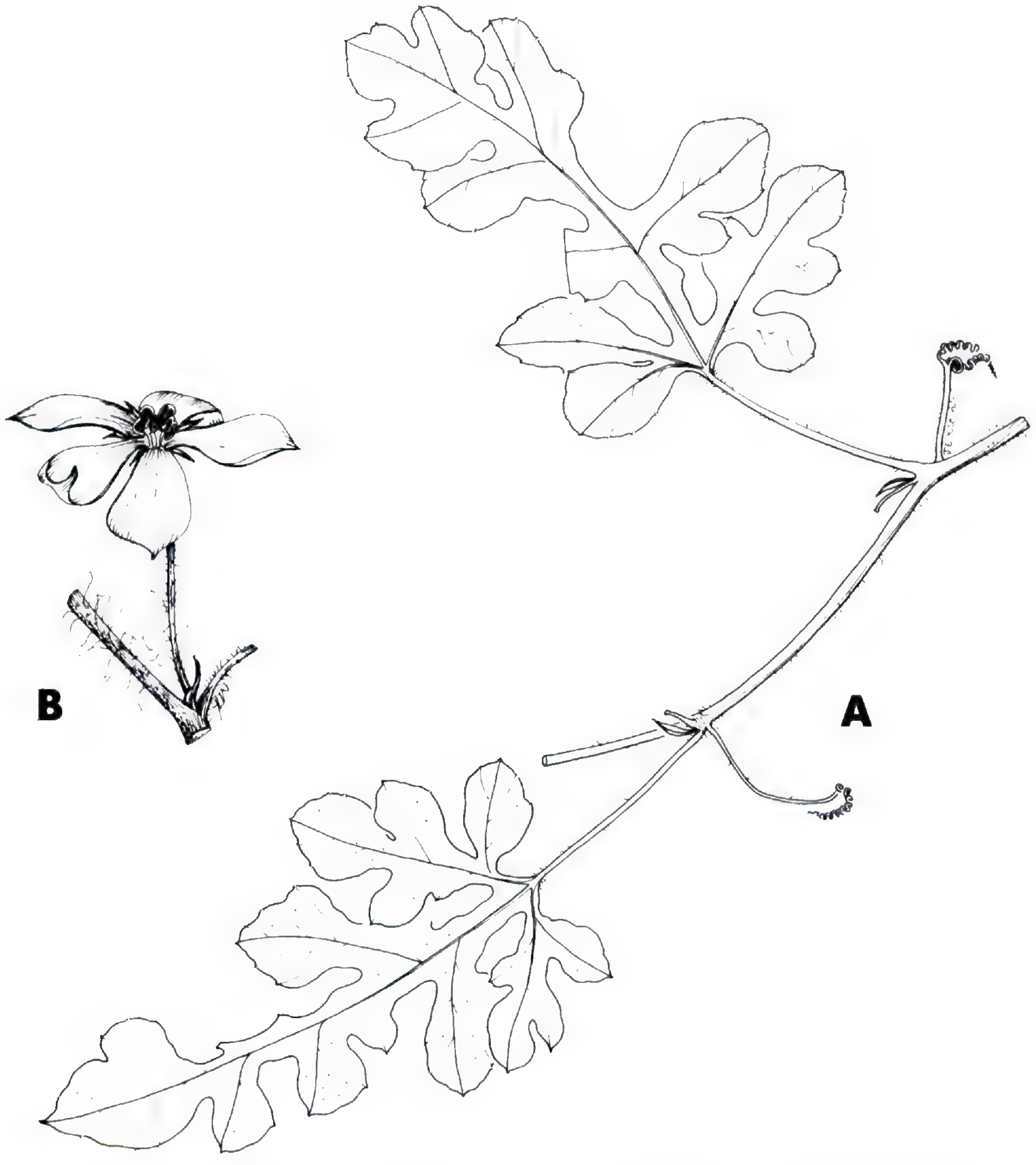


FIGURE 3. *Citrullus lanatus* (Thunb.) Mats. & Nakai.—A. Habit (×3/5). [After *Gentry* 5559]—B. Flower (×9/10). [After *Hood* 1910—Florida].

diverging, the anthers ca. 3 mm long; pistillodium glanduliform. *Pistillate flowers* similarly disposed as the staminate flowers; calyx and corolla as in the staminate; ovary ovoid, the style column slender, the stigmas short, the lobes spreading; staminodia setiform, villous at the base. *Fruits* green, mottled, or striped with dark and light green, globose to oblong, white within, the outer rind hard, the inner flesh pink or yellow, smooth, glabrous; seeds numerous, elliptical, 3–12 mm long, dirty white to black or mottled, smooth or nearly so.

The "common watermelon" or "sandia," native to Africa, is widely cultivated

for its edible fruits. Although it is often spontaneous in waste ground, such plants rarely produce mature fruits. Numerous varieties differing widely in fruit characteristics are grown in Panama and elsewhere.

Although this species is undoubtedly more common, only the following specimens have been examined from Panama.

PANAMÁ : N of El Llano, *Gentry 5559* (F, GH, MO, NY). Sabanas, N of Panama City, *Paul 548* (US). E edge of Panama City, *Sauer 2320* (F).

4. CUCUMIS

Cucumis L., Sp. Pl. 1001. 1753; Gen. Pl., ed. 5. 442. 1754. LECTOTYPE: *C. sativus* L.

Melo Miller, Gard. Dict., abr. ed. 4. 1754. TYPE: *Cucumis melo* L.
Rigocarpus Neck., Elem. Bot. 1: 238. 1790. TYPE: not designated.

Monoecious, trailing, tendriled *vines*; stems 5- to 10-sulcate. *Leaves* petiolate, lobed or angular; tendrils simple, sometimes straight and spinescent. *Staminate flowers* axillary; fasciculate or solitary; calyx turbinate or campanulate, 5-lobate; corolla campanulate, 5-lobate; stamens 3, borne on the hypanthium wall, the filaments free, stout, the anthers curved or flexuous, one anther unilocular, the other anthers bilocular, connective with 2-lobed appendage; pistillodium gland-like. *Pistillate flowers* similarly disposed as the staminate flowers; calyx and corolla as in the staminate flowers; ovary globose or oblong, 3-carpellate, the styles 3–5, connate, short, the stigmas connate, 3–5, forming a spherical or obovate head; staminodia 3, small. *Fruits* fleshy, the surface smooth or roughened, usually indehiscent; seeds numerous, horizontal, ovate to oblong, compressed, emarginate, the testa smooth.

Cucumis is a genus of about 25 species, mainly Old World tropics and subtropics with four species found in Panama.

Literature:

Cogniaux, A. & H. Harms. 1924. Cucurbitaceae: Cucurbiteae—Cucumerinae *in* A. Engler. Das Pflanzenreich 88 (IV, Fam. 275, II): 1–246.

a. Ovary hispid to tuberculate; fruit densely to sparingly armed.
  b. Leaves deeply 3- to 5-lobate ..... 1. *C. anguria*
  bb. Leaves entire to shallowly lobed.
    c. Fruit densely spiny ..... 2. *C. dipsaceus*
    cc. Fruit sparingly spiny or tuberculate ..... 4. *C. sativus*
aa. Ovary pubescent; fruit unarmed ..... 3. *C. melo*

1. **Cucumis anguria** L., Sp. Pl. 1011. 1753. SYNTYPES: without locality, Herb. Linn. 1152.5 & 1152.6 (LINN, neither seen; microfiche MO).—FIG. 4.

C. echinatus Moench, Meth. Pl. 654. 1794. TYPE: not known.
C. parviflorus Salisb., Prodr. Stirp. 157. 1796. TYPE: not known.
C. angurioides Roem., Fam. 2: 27. 1846. [1847] TYPE: not known.
C. arada L. ex Naud. & F. Muell., Man. Accl. 230. 1887. TYPE: not known.

Prostrate *vines*; stems hispid or scabrous with pustulate based trichomes. *Leaves* broadly ovate or suborbicular, 5–10 cm long, nearly or equally as wide as long, deeply 3- to 5-lobate, the lobes obtuse at the apex, cordate or subtruncate

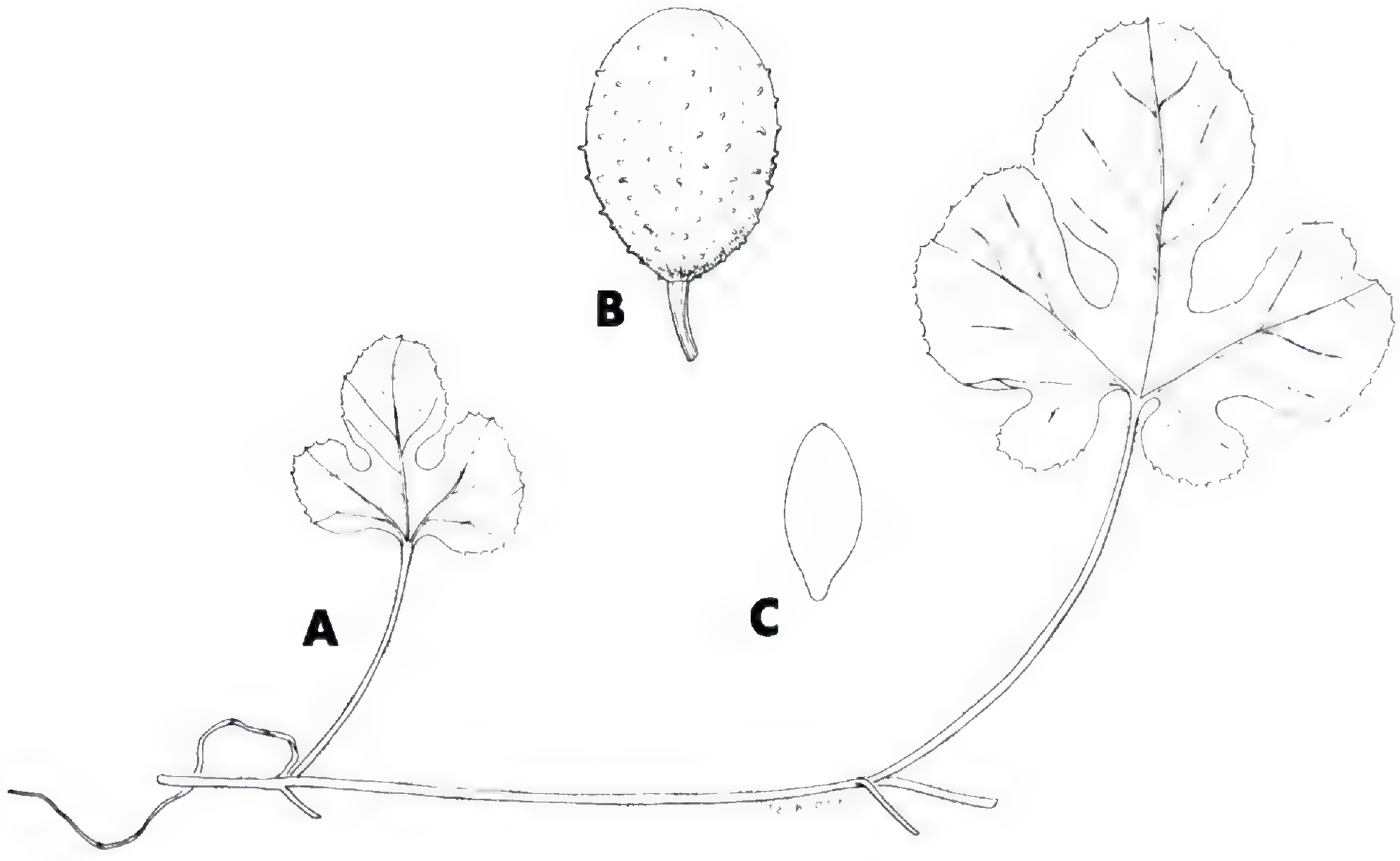


FIGURE 4. *Cucumis anguria* L.—A. Habit (×½).—B. Fruit (×½). [After *Romero-Castañeda 10464*—Colombia].—C. Seed (×2½). [After *Tyson et al. 3000*].

at the base, the middle lobe obovate, the lateral lobes various, usually oblique, the sinuses rounded, the margin undulate dentate, chartaceous, both the surfaces hispid or scabrous; petiole 3–8 cm long, hispid or scabrous. *Staminate flowers* axillary, fasciculate or sometimes solitary, short pedunculate; calyx campanulate, the lobes 3–4 mm long, subulate, hispid green; corolla campanulate, the lobes ca. 5 mm long, yellow, obovate, the apex acute, spreading; stamens 3–4 mm long, glabrous, the anthers ca. 2 mm long, the appendix of the connective dilated, deeply 2-lobed, 1–2 mm long, the segments bilobate; pistillode glandlike. *Pistillate flowers* solitary in the same axils as the staminate flowers; peduncle 4–15 cm long; calyx and corolla as in the staminate flowers; ovary oblong; hispid; stigmas forming a spherical head. *Fruits* yellow, sometimes with lighter longitudinal stripes, ellipsoidal or ovoid, 4–7 cm long, 3–6 cm in diameter, sparsely prickly with rigid spines; seeds numerous, horizontal, dirty white, oblong, 4–5 mm long, 2.0–2.5 mm wide, the testa smooth or nearly so.

Cucumis anguria is found in thickets and waste ground throughout much of the tropics and subtropics in the New World. In Panama it is known from a single collection, but doubtlessly is more common than collections indicate.

This species is known throughout its range by various common names: "anguria," "pepino cimarron," "pepineto," "concombro," "bur cucumber," "West Indian gherkin," or "gooseberry gourd." In Guatemala it is called "sandia de raton." It is grown in Panama and elsewhere as an oddity or for its fruit which can be made into pickles or boiled and used in salads.

LOS SANTOS: Managre Beach, 5 mi SE of Chitré, *Tyson et al. 3000* (MO).

2. **Cucumis dipsaceus** Ehrenb. in Spach, Hist. Nat. Vég. Phan. 6: 211. 1838. TYPE: not known.

C. bardana Fenzl. ex Naud., Ann. Sci. Nat. Bot. sér. 11. 4: 25. 1859. TYPE: not known.
C. ambigua Fenzl. ex Hook. f. in Oliver, Fl. Trop. Afr. 2: 543. 1871, *pro part.* TYPE: not known.
C. dasycarpa Hochst. ex A. Rich., Tent. Fl. Abyss. 1: 291. 1817. TYPE: not known.

Vines; stems hispid. *Leaves* suborbicular to reniform, 5–10 cm long, as broad or broader than long, slightly 3- to 5-angulate, the base cordate, the apex of the lobes rounded, the margin dentate, membranaceous or chartaceous, both surfaces hispid or scabrous; petiole 5–12 cm long, hispid. *Staminate flowers* axillary, solitary or fasciculate; peduncle 0.5–2.0 cm long; calyx subcylindrical, the lobes ca. 2 mm long, subulate, hirsute, green; corolla campanulate, the lobes 6–8 mm long, yellow, oblong, the apex acute, spreading; stamens ca. 3–4 mm long, the anthers 2–3 mm long, the appendix of connective dilated, bilobate, ca. 1 mm long, the apex ciliate; pistillodium glandlike. *Pistillate flowers* solitary in the same axils as staminate flowers; peduncles 1–2 cm long; calyx and corolla as in the staminate flowers; ovary oblong, densely hispid; style 1–2 mm long; stigma forming a spherical head. *Fruit* pale yellow, ovoid cylindrical 3–8 cm long, 2–5 cm in diameter, densely spiny; seeds pale brown, oblong, compressed, 4.0–5.0 mm long, 2 mm wide.

Native to the Old World tropics, this species is sparing naturalized in the Neotropics, occurring in dry, disturbed thickets, old fields, and roadsides. Panamanian specimens have been seen from Darién and the Canal Zone, but it is likely to be encountered elsewhere.

Cucumis dipsaceus is called the hedgehog cucumber or Pepino diablito.

CANAL ZONE: Coastal island beyond Fort Amador, *D'Arcy* 9227 (MO). DARIÉN: Without other locality, *Bristan* 5 (MO).

3. **Cucumis melo**[5] L., Sp. Pl. 1011. 1753. TYPE: without locality, Herb. Linn. 1152.8 (LINN, not seen; microfiche MO).

Vines; stems hispid or scabrous. *Leaves* suborbicular to ovate, 5–15 cm long and wide, shallowly 3–7-lobate, the apex of the lobes rounded, the base cordate, the margin shallowly undulate denticulate, chartaceous, both the surfaces hispid or scabrous; petiole 5–15 cm long, hispid or scabrous. *Staminate flowers* axillary, fasciculate; peduncle 0.5–2.0 cm long; calyx subcylindrical, lobes 4–6 cm long, subulate, hirsute, green; corolla campanulate, the lobes ca. 1 cm long, yellow, oblong, the apex acute; stamens 6–8 mm long, the anthers 3–4 mm long, the appendix of connective dilated, bilobate; pistillode glandlike. *Pistillate flowers* in same axils as the staminate flowers; peduncles 1–2 cm long; calyx and corolla as in the staminate flowers; ovary ovoid to subcylindrical, tomentose, the style 1–2 mm long, the stigma forming a spherical head. *Fruit* variable in color, usually globose, smooth or reticulate, variable in size, glabrous or pubescent; seeds grayish white, oblong, compound, 7–12 mm long, 4–7 mm wide.

[5] For the extensive synonymy of this species, see Cogniaux and Harms (1924).

The melon, muskmelon, or cantaloupe, native to the Old World tropics, is widely cultivated for food in temperate and tropical regions throughout the world. It frequently persists after cultivation or as an escape in ruderal areas.

This is a highly variable species with numerous described wild and cultivated varieties. The taxonomy is much in the need of revision.

PANAMÁ: Panama Viejo, *Bristan P/12* (MO).

4. **Cucumis sativus**[6] L., Sp. Pl. 1012. 1753. TYPE: not known.

Vines; stems hirsute or scabrous. *Leaves* cordate, 12–18 cm long and wide, angulate or shallowly 3- to 5-lobate, the apex of the lobes acute, the base cordate, the margin denticulate, chartaceous, both surfaces hispid or scabrous; petiole 5–15 cm long, hispid or scabrous. *Staminate flowers* axillary, fasciculate; peduncle 0.5–2.0 cm long; calyx subcylindrical, the lobes 4–6 mm long, subulate, villous, green; corolla campanulate, lobes ca. 2 cm long, yellow, ovate lanceolate, acute; stamens 6–8 mm long, the anthers 3–4 mm long, the appendix connective ca. 1 mm long; pistillode glandlike. *Pistillate flowers* in same axils as the staminate flowers; peduncles 1–2 cm long; calyx and corolla as in the staminate flowers; ovary fusiform, tuberculate, the style 1–2 mm long, the stigma forming a spherical head. *Fruit* yellowish, usually cylindrical or oblong, tuberculate, glabrous; seeds whitish, oblong, 8–10 mm long, 3–5 mm wide.

This species, the common cucumber, native to the Old World tropics, is widely cultivated for food in temperate and tropical regions throughout the world. It frequently persists after cultivation or as an escape in ruderal areas. No specimens have been seen from Panama, but it is to be expected.

It is a highly variable species with numerous described cultivated varieties. The taxonomy is much in the need of critical study.

This species is known as "pepino," "pepino de ensalada," "pepino de Espana," and "cohombro" in the American tropics.

5. CUCURBITA

Cucurbita L., Sp. Pl. 1010. 1753; Gen. Pl. ed. 5. 441. 1754. LECTOTYPE: *C. lagenaria* L.

Melopepo Miller, Gard. Dict. abr. ed. 4. 1754. TYPE: not designated.
Pepo Miller, Gard. Dict. abr. ed. 4. 1754. TYPE: not designated.
Sphenantha Schrad., Linnaea 12: 416. 1838. TYPE: *S. scabra* Schrad.
Pileocalyx Gasp., Ann. Sci. Nat. Bot. sér. 3. 9: 220. 1848. TYPE: *P. elegans* Gasp.
Tristemon Scheele, Linnaea 21: 586. 1848, non Raf., 1819 (Juncaginaceae), nec Raf., 1838 (Juncaceae), nec Kotz., 1838 (Ericaceae). TYPE: *T. texanum* Scheele.

Annual or perennial, monoecious, tendriled *vines*; stems 5- to 10-sulcate, usually creeping. *Leaves* subentire and reniform or suborbicular to deeply pinnate or bipinnately divided; tendrils 2- to 5-branched. *Staminate flowers* solitary or fasciculate; calyx campanulate, rarely cylindrical, 5-lobate (rarely 4- to 7-lobate); corolla campanulate, 5-lobate (rarely 4- to 7-lobate) to or below

[6] For the extensive synonymy of this species, see Cogniaux and Harms (1924).

the middle, the apex of the lobes recurved; stamens 3, inserted on the hypanthium tube, the filaments free, the anthers linear, connate into a cylindrical column, 1 anther unilocular, 2 anthers bilocular, the theca flexuous; peduncle short. *Pistillate flowers* solitary, axillary, short pedunculate; calyx and corolla as in the staminate flowers; ovary oblong, 3- to 5-locular, the ovules numerous, horizontal, the styles short, thick, the stigmas 3–5, bilobate or bifurcate, papillose; staminodia 3, triangular. *Fruits* fleshy and fibrous, sometimes woody, indehiscent, highly variable in shape, size, and color; seeds ovate or oblong, flattened, the margins tumid or emarginate, the testa smooth.

The genus *Cucurbita*, with perhaps as many as 27 species, is native to the Neotropics although several species are much cultivated and consequently widely distributed in both the Old and New World. The center of origin for the genus is apparently southern Mexico and northern Central America where most wild and cultivated species still grow. The oldest archeologically known species is *C. pepo* (Cutler & Whitaker, 1961). Specimens of this species were found in caves in Mexico and date back to approximately 7000 B.C.

Five species of *Cucurbita* are commonly cultivated, each with several races or varieties: *C. pepo* L., *C. moschata* Duch. ex Poit., *C. maxima* Duch., *C. mixta* Pang., and *C. ficifolia* Bouché.

The common terms pumpkin and squash are of little value in differentiating among species of *Cucurbita*. Both terms are used for cultivars of *C. pepo*, *C. maxima*, *C. mixta*, and *C. moschata* in addition to a few other species of the genus. Similarly, the term gourd is applied to cultivars of *C. pepo*, *C. ficifolia*, and *C. mixta*, as well as to other species of *Cucurbita* and to *Lagenaria siceraria* (bottle gourd). It is also applied to species other than the Cucurbitaceae (e.g. *Crescentia cujete* L., calabash tree or gourd tree—Bignoniaceae).

In Panama the most commonly cultivated *Cucurbita* species is probably *C. moschata*. *Cucurbita pepo* and *C. maxima* are believed to be more recent introductions into the country and are less common. *Cucurbita ficifolia*, although probably introduced very early, is not cultivated as frequently as the other three species. Finally, *C. mixta* may also be encountered in cultivation in Panama.

Since the five species of *Cucurbita* are found in Panama primarily as cultivated plants, rarely as escapes and probably not naturalized, they will only be briefly listed in this treatment.

Literature:

Bailey, L. H. 1943. Species of *Cucurbita*. Gentes Herb. 4: 267–316.
Bukasov, S. M. 1930. The cultivated plants of Mexico, Guatemala, and Colombia. Trudy Prikl. Bot. Suppl. 47: 1–553.
Cutler, H. C. & T. W. Whitaker. 1961. History and distribution of the cultivated cucurbits in the Americas. Amer. Antiquity 26: 469–485.

1. **Cucurbita ficifolia** Bouché, Verh. Ver. Gartenb. Berlin 12: 205. 1837. TYPE: not known.

C. melanosperma Gaspar., Ann. Sci. Nat. Bot. sér. 4. 9: 208. 1855. TYPE: not known.

This species is commonly known as the "chilacayote" in the American tropics. It is also called the "malabar gourd" or "fig-leaf gourd." It is cultivated in Mexico, the Caribbean, and as far south as Bolivia for its edible fruit, mostly at middle and high elevations. It is locally naturalized in much of its range. The fruits are cooked in a heavy syrup and eaten as deserts. No specimens have been seen from Panama, but it is to be expected as an escape.

2. **Cucurbita maxima**[7] Duch. in Lam., Encyc. Méth. Bot. 2: 251. 1786. TYPE: not known.

This is the "autumn" or "winter squash" and "pumpkin" of cultivation. Numerous cultivars are grown. No specimens have been seen from Panama, but the species is cultivated for its edible fruit there, and is to be expected as spontaneous after cultivation or as an occasional escape.

3. **Cucurbita mixta** Pang. Trudy Prikl. Bot. Selekc. 1929–1930. 23: 264–1930. TYPE: not known.

C. argyrosperma L. H. Bailey, Gentes Herb. 7: 457. 1948. TYPE: not known.

This is the "winter squash," "pumpkin," "cushaw," and "silver-seed gourd" of cultivation. No specimens have been seen from Panama, but the species is occasionally cultivated for its edible fruits and is to be expected as spontaneous after cultivation or as an escape.

4. **Cucurbita moschata**[8] Duch. ex Poir., Dict. Sci. Nat. 11: 234. 1818. TYPE: not known.

This species is the "pumpkin," "winter crookneck," and "winter squash" of cultivation. Although no specimens were seen from Panama, the species is cultivated for its edible fruit and is to be expected as spontaneous after cultivation or escaped. This species is the only one collected by the Russian plant collecting expedition in Panama (Bukasov, 1930).

5. **Cucurbita pepo**[9] L., Sp. Pl. 1010. 1753. TYPE: without locality, Herb. Linn. 1151.4 (LINN, not seen, microfiche MO).—FIG. 5.

This species includes the "summer squash," "summer crookneck squash," "summer pumpkin," "common gourd," "marrow," "zucchini," and numerous other cultivars. This and probably other species of *Cucurbita* in Panama are known as "supuyo" or "calabazo." Specimens are occasionally found as spontaneous in waste ground. It is not known in the wild state.

CHIRIQUÍ: Camino que va desde el pueblo de Cerro Punta a la zona maderera de Las Nubes, *Correa 1329* (MO). On mountains above Bambito, 1 mi S of Cerro Punta, *Tyson 5775* (MO). Bajo Chorro, *Woodson & Schery 617* (MO). DARIÉN: Forest along road to Pinogana near El Real, *Croat & Porter 15471* (MO). PANAMÁ: Panamerican Highway just W of La Chorrera, *D'Arcy 9615* (MO). Interamerican Highway just E of Bejuco, *Duke 4553* (MO). Near Río Bayano Dam site, *Gentry 6445* (F, MO, NY). 1 mi W of Bejuco along Panamerican Highway, *Tyson & Blum 2536* (FSU, MO).

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[7] See Cogniaux (1881: 544–545) for synonymy.
[8] See Cogniaux (1881: 547) for synonymy.
[9] See Cogniaux (1881: 545–546) for synonymy.

FIGURE 5. *Cucurbita pepo* L. Habit (×⅗). [After *Gentry 6445*].

6. CYCLANTHERA

Cyclanthera Schrad., Ind. Sem. Hort. Götting. 1831: 2. 1831. TYPE: *C. pedata* Schrad.

Discanthera Torr. & Gray, Syn. Fl. N. Amer. 1: 696. 1840. TYPE: *D. dissecta* Torr. & Gray.

Monoecious, tendriled *vines*; stems 5- to 10-sulcate. *Leaves* petiolate, simple to pedately 3- to 5-foliolate, with or without glands at base; tendrils simple or to 5-branched. *Staminate flowers* in racemes or narrow panicles, axillary; calyx cupulate, 5-lobate; corolla greenish-yellow or white, rotate, 5-lobate; stamen 1, the anther forming a capitate horizontal ring, the theca unilocular. *Pistillate flowers* solitary or few in same axils as the staminate flowers, but larger; ovary obliquely ovoid, rostrate, 1–3 carpellate, the style 1, the stigma subglobose. *Fruit* obliquely ovoid, often echinate, explosively dehiscent or indehiscent; seeds few to many, erect, ovoid to angular, somewhat compressed, the margin often appendaged, the testa rugose or smooth.

Cyclanthera is a genus of about 20 species distributed from southern United States to Argentina. Three species are reported from Panama. Two additional species are to be expected, both having been reported from adjacent Costa Rica and Colombia.

a. Leaves 3- to 5-foliolate.
  b. Leaves distinctly 3-foliolate ..... 4. *C. multifoliola*
  bb. Leaves 5-foliolate (sometimes 3-foliolate and 5-segmented).
    c. Fruits 5–16 cm long, smooth or only slightly echinate, indehiscent .. 5. *C. pedata*

cc. Fruits 2.0–2.5 cm long, conspicuously echinate, explosively dehiscent ..... 1. *C. dissecta*

aa. Leaves simple.
d. Staminate inflorescences arising from the petiole at base of leaf blade .. 2. *C. dressleri*
dd. Staminate inflorescence arising from the axis of subtending leaf ..... 3. *C. explodens*

1. **Cyclanthera dissecta** (Torr. & Gray) Arn. & Hook. J. Bot. (Hooker), 3: 280.

Discanthera dissecta Torr. & Gray, Syn. Fl. N. Amer. 1: 696. 1840. TYPE: not known.
Echinocystis pedata Scheele, Linnaea 21: 587. 1848. TYPE: not known.
Cyclanthera naudiniana Cogn. in DC., Monogr. Phan. 3: 831. 1881. LECTOTYPE: Texas, *Lindheimer 398* (MO, isolectotype).
Cyclanthera naudiniana var. *tenuifolia* Cogn. in DC., Monogr. Phan. 3: 832. 1881. TYPE: Mexico, *Muller 589* (K, holotype, not seen).

Vines; stems slender, glabrous. *Leaves* 5-foliolate, sometimes the two lateral lobes slightly joined at the base and the leaves 3-foliolate, the blade suborbicular in outline, 2–4 cm wide and long, the leaflets lanceolate, the lateral leaflets often pedately lobate, the margins coarsely crenate-serrulate, the apex acute, membranaceous, the upper surface scabrellous, the lower surface glabrate; petiole 2–5 cm long, slender; tendrils simple. *Staminate flowers* axillary, elongate-paniculate; rachis 15–25 cm long, slender, flowered only on the upper half, the flowers often in subumbelloid clusters; pedicels 3–6 mm long, filiform; calyx shallowly capulate, 3–5 mm wide, greenish-white, the lobes minute, subulate; corolla ca. 6 mm in diameter, the white or cream lobes 2.0–2.5 mm long, lanceolate, the outer surface glabrous, the inner surface slightly papillate, 3-nerved; androecial head subsessile, 0.5–1.0 mm in diameter. *Pistillate flowers* solitary, in same axis as the staminate flowers; peduncles 2–15 mm long; calyx and corolla as in the staminate flowers but slightly smaller; ovary obliquely ovoid, rostrate, ca. 2 mm long; setose, the stigma subglobose. *Fruits* greenish, obliquely ovoid, 1.5–2.0 cm long, explosively dehiscent, the seta 5–7 mm long; in outline, 2–4 cm wide and long, the leaflets lanceolate, the lateral leaflets often seeds grayish brown, ovoid, compressed, the margin irregularly appendaged.

This species ranges from southwestern United States south through Central America, occurring in moist to dry thickets. In Panama it is known only from the Canal Zone, but doubtlessly occurs elsewhere. It has previously been reported from Panama by Cogniaux (1881) as *C. naudiniana.*

CANAL ZONE: Ancón Hill, *Heriberto 128* (GH, US); *Killip 12083* (NY, US); *Standley 25190, 26322* (both US). Sosa Hill, Balboa, *Standley 26428* (US).

2. **Cyclanthera dressleri** Wunderlin, Phytologia 38: 219. 1978. TYPE: Panama, *Mori & Dressler 7795* (MO, holotype; USF, isotype).

Vines; stems slender, glabrous. *Leaves* simple, the blade hastate, 5–9 cm long, 3–6 cm wide at base, the margins denticulate, the apex acuminate, the basal sinus acute, chartaceous, the upper surface minutely pustulate, the lower surface glabrous; petiole 1.5–2.0 cm long; tendrils simple. *Staminate flowers* produced from the petiole at the base of the leaf blade, short racemose, 6–10-flowered; peduncle 1.5–2.0 cm long, slender; pedicels 5–8 mm long, filiform; calyx shallowly cupulate, 3–5 mm wide, greenish-white, the lobes obsolete; corolla ca. 6 mm in diameter, white or cream, the lobes 2–3 mm long, broadly lanceolate or

triangular, the outer surface glabrous, the inner surface slightly papillate, 3-nerved; androecial column ca. 1 mm long, head ca. 1 mm in diameter. *Pistillate flowers* solitary in same axils as staminate flowers; peduncle 6–10 mm long; calyx and corolla as in the staminate flowers, but slightly smaller; ovary obliquely ovoid, rostrate, ca. 4 mm long, short setose; stigma subglobose. *Fruits* greenish, obliquely ovoid, ca. 1.5 cm long, explosively dehiscent, seta ca. 1 mm long; seeds not seen.

A rare species known only from the type locality, Cerro Colorado, Chiriquí Province. It occurs in the cloud forest at 1,200–1,500 m elevation.

CHIRIQUÍ: Cerro Colorado, 50 km N of San Félix on the Continental Divide, *Mori & Dressler 7795* (MO, USF). N of San Félix at Chiriquí-Bocas del Toro border, on Cerro Colorado copper mine road along continental divide, *Mori & Kallunki 5925* (MO, USF).

3. **Cyclanthera explodens** Naud., Ann. Sci. Nat. Bot. sér. 4. 12: 160. 1859. TYPE: not known.

C. explodens var. *intermedia* Cogn. ex Kuntze, Rev. Gen. Pl. 3: 103. 1898. TYPE: not known.
C. explodens var. *trifida* Cogn. ex Kuntze, Rev. Gen. Pl. 3: 103. 1898. TYPE: not known.

Vines; stems slender, glabrate, often puberulent at the nodes. *Leaves* simple, ovate to suborbicular, 3- to 5-lobate, 5–10 cm long and wide, the margins denticulate, the apex acute, the base shallowly to deeply cordate, submembranaceous to chartaceous, the upper and the lower surfaces pustulate, puberulent on the nerves; petiole 1.5–3.0 cm long, glabrate; tendrils unequally 2-branched. *Staminate flowers* axillary, short racemose, delicate, 8- to 10-flowered; peduncle usually less than 1 cm long, puberulent; pedicels 2–4 mm long, filiform; calyx shallowly cupulate, 1.0–1.5 mm wide, greenish white, the lobes obsolete; corolla ca. 1.5–2.5 mm wide, white, the lobes broadly lanceolate, the outer surface glabrous, the inner surface papillate, 3-nerved; androecial head subsessile, ca. 0.5 mm in diameter. *Pistillate flowers* solitary, in same axils as staminate flowers; peduncle 1–2 mm long, puberulent; calyx and corolla as in the staminate flowers; ovary obliquely ovoid, rostrate, 4–6 mm long, with a few seta 1–2 mm long; stigma subglobose. *Fruits* greenish, obliquely ovoid, 2–4 cm long, explosively dehiscent, with few scattered seta 4–5 mm long; seeds grayish brown, ovoid, compressed 7–9 mm long, the margin slightly appendaged.

This species ranges from Mexico south to Colombia, occurring in thickets from 800–2,000 m elevation. Although unreported from Panama, it is to be expected. This species is often cultivated for its edible fruits.

4. **Cyclanthera multifoliola** Cogn., Mem. Couronnés Acad. Roy. Sci. Bruxelles, sér. 4, 28: 66. 1877. TYPE: not known.—FIG. 6.

Cyclanthera filifera Cogn. Mem. Couronnés Acad. Roy. Sci. Bruxelles, sér. 4, 28: 72. 1877. TYPE: not known.

Annual *vines*; stem puberulent to glabrate. *Leaves* 3-foliolate, lateral leaflets 3- to 7-times dissected, blade suborbicular, 3.5–15.0 cm long, 4.5–20.0 cm wide, the leaflets or ultimate divisions elliptic, the margins coarsely serrate dentate, the apex acute, membranaceous, the upper and lower surfaces scabrellous to

FIGURE 6. *Cyclanthera multifoliola* Cogn. Habit (×7/10). [After *Burch 2712*—Mexico].

glabrate; petiole 2–4 cm long, slender, glabrate; tendrils 3- to 5-branched. *Staminate flowers* axillary, elongate paniculate; rachis 15–30 cm long, slender, flowering along most of its length; pedicels 1–3 mm long, filiform; calyx shallowly cupulate, 0.8–2.5 mm in diameter, greenish white, the sepals obscure; corolla 2.0–3.5 mm in diameter, greenish white, lobes ca. 1 mm long, broadly lanceolate, the outer surface glabrous, the inner surface papillate, 3-nerved; androecial head sessile, ca. 1 mm in diameter. *Pistillate flowers* solitary, in the same axils as the staminate flowers; peduncle 0.5–2.0 cm long; calyx and corolla as in the staminate flowers but slightly smaller; ovary obliquely ovoid, rostrate, ca. 8 mm long, setose; stigma subglobose. *Fruits* greenish white, obliquely ovoid, 3–4 cm long, explosively dehiscent, seta 5–7 mm long; seeds grayish brown, ovoid, compressed, 8–13 mm long, the margin irregularly appendaged.

This species occurs in thickets and forest edges at 100–1,500 m elevation from Mexico south to Peru. No specimens have been seen from Panama, but it is to be expected.

5. **Cyclanthera pedata** (L.) Schrad., Linnaea 8, Litt.-Bericht.: 23. 1833.

Momordica pedata L., Sp. Pl. 2: 1009. 1753. TYPE: not known.
Anguria pedatisecta Nees & Mart., Nova Acta Caes. Leop. Carol. German Nat. Cur. 12: 10. 1824. TYPE: not known.
A. pedisecta Ser. in DC., Prodr. 3: 319. 1828, non Nees & Mart., 1824. TYPE: not known.
Momordica pedisecta Ser. in DC., Prodr. 3: 319. 1828, pro syn.
Cyclanthera digitata Arnott, J. Bot. (Hooker) 3: 280. 1841. TYPE: not known.
C. edulis Naud., Belgique Hort. 360. 1872. TYPE: not known.
C. pedata var. *edulis* (Naud.) Cogn. in DC., Monogr. Phan. 3: 826. 1881.

Annual *vines*; stems slender, glabrous. *Leaves* 5-foliolate, sometimes the two lateral lobes slightly joined at the base and the leaves 3-foliolate, the blade suborbicular in outline, 2.5–20 cm long and about as wide, the leaflets lanceolate, the lateral leaflets often pedately lobate, the margins serrulate-dentate to dissected, the apex acute, membranaceous, the upper and the lower surfaces glabrate; petiole 1–8 cm long; tendrils 2-branched. *Staminate flowers* axillary, paniculate; rachis 10–20 cm long, the 25(–50) flowers confined to the upper ½–¼ of the rachis; pedicels ca. 5 mm long, filiform; calyx shallowly cupulate, 3–4 mm wide, greenish white, the lobes obscure or to 2 mm long; corolla 3–6 mm wide, whitish, the lobes 1–2 mm long, broadly lanceolate, the outer surface glabrous, the inner surface papillate, 3-nerved; androecial head sessile, 2.0–2.5 mm in diameter. *Pistillate flowers* solitary, in the same axils as the staminate flowers; peduncle 6–10 mm long; calyx and corolla as in the staminate flowers; ovary obliquely ovoid, rostrate, 4–6 mm long, unarmed or with a few seta near the base; stigma subglobose. *Fruits* greenish white, striate, obliquely ovoid, 5–16 cm long, indehiscent, the setae few or none; seeds dark brown, ovoid, compressed, 12–16 mm long, the margin irregularly appendaged.

Cyclanthera pedata occurs in thickets and disturbed sites around habitations from Mexico south to Peru and Ecuador. It is probably native to Andean South America, but is commonly cultivated in the Neotropics for its edible fruit and it frequently occurs as an escape. It is reported by Standley (1928) as occurring in the Canal Zone of Panama. Although no specimens have been seen, it is to be expected.

7. ELATERIOPSIS

Elateriopsis Ernst., Flora 56: 257. 1873. TYPE: *E. caracasana* Ernst.

Monoecious, tendriled *vines*; stems 5-sulcate. *Leaves* petiolate, entire, angulate, or 3- to 5-lobate; tendrils 3- to 5-branched. *Staminate flowers* in axillary racemes; calyx campanulate, 5-lobate; corolla campanulate or spreading, 5-lobate; stamens 5, the filaments connate, the anthers connate, conduplicate, forming a subspherical head. *Pistillate flowers* solitary in the same axils as the staminate flowers; calyx and corolla as in the staminate flowers; ovary ovoid to fusiform, usually oblique, 3-carpellate, the styles 4, connate, erect, the stigmas 3, forming a peltate, irregularly-lobate head. *Fruits* ovate to fusiform, usually oblique, longitudinally dehiscent, with or without spines, usually fleshy; seeds several in each carpel, pendulous, subovate to obtusely triangular, compressed, the margins often undulate or notched, the testa smooth or rugulose.

Elateriopsis includes about five species in the Neotropics, a single species occurring in Panama.

Literature:

M. Crovetto, R. 1957. Revision critica del genero "*Elateriopisis*." Darwinia 11: 23–243.

1. **Elateriopsis oerstedii** (Cogn.) Pittier, Contr. U.S. Natl. Herb. 13: 125. 1910. —FIG. 7.

Cyclanthera oerstedii Cogn. in DC., Monogr. Phan. 3: 856. 1881. SYNTYPES: Costa Rica, *Oersted 18, 19, 20* (all BR, none seen).
Elateriopsis oerstedii var. *biolleyi* Cogn. ex Pittier, Contr. U.S. Natl. Herb. 13: 126. 1910. TYPE: Costa Rica, *Biolley* (CR, holotype, not seen; US, isotype).

Scrambling *vines*; stems glabrous or puberulent in furrows. *Leaves* simple, broadly triangular cordate, angulate or obscurely 3-lobate, 6–15 cm long, 7–8 cm wide, the apex acuminate, the base cordate, the margin entire or with remote, minute teeth, chartaceous, the upper surface minutely pustulate, the lower surface puberulent on the nerves, at least near the base; petiole 3–8 cm long, slender, striate; tendrils 2- to 4-branched near the middle. *Staminate flowers* axillary, racemose; rachis 5–25(–40) cm long, slender, usually flowered only in the upper ⅓, puberulent in upper ⅓; pedicels 5–25 mm long, filiform; calyx broadly campanulate, green, puberulent, densely ciliate on the rim, the lobes subulate, ca. 1 mm long, acuminate, reflexed or spreading; corolla lobes ovate lanceolate, 5–10 mm long, greenish white, the apex obtuse, puberulent on both the surfaces, densely ciliate, 7-nerved for most their length; filament column 2–3 mm long, the anthers forming a depressed, subspherical head 5–10 mm wide. *Pistillate flowers* solitary in the same axils as the staminate flowers; peduncle ca. 1 cm long, slender, puberulent; calyx and corolla similar to that of the staminate flowers; ovary obliquely fusiform, 8–10 mm long, puberulent, the beak ca. 5 mm long, styles 3, ca. 2 mm long, connate, the stigmas forming a capitate, 3-lobate head 5–8 mm in diameter. *Fruits* light green with darker longitudinal lines, drying reddish, flesh white, obliquely subconic, apex prolonged and usually arcuate, 6–8 cm long, 3–4 cm in diameter, surface smooth, glabrate, elastically and longitudinally dehiscent; seeds, obovate, 18–25 mm long, 15–20 mm wide, compressed, the apex entire or with 2–3 notches, the base with a single notch, brownish, the testa rugulose.

This species occurs in open woods, thickets, and disturbed sites from sea level to approximately 1,400 m. It is reported only from Costa Rica and Panama.

Elateriopsis oerstedii var. *biolleyi* intergrades with the typical variety and cannot be retained as a distinct taxon.

BOCAS DEL TORO: Santa Catalina, *Blackwell et al. 2689, 2753* (both MO). Río Teribe between Río Treglo and Puerto Palenque, *Kirkbride & Duke 530* (MO). Fish Creek Mountains, Chiriquí Lagoon, *Wedel 2288* (GH, MO). COCLÉ: El Valle de Antón and vicinity, *Croat 13382* (DUKE, MO, USF), *14267* (F, MO, US); *Dwyer & Nee 11942* (MO); *Gentry 5631* (F, MO); *Hunter & Allen 363* (MO); *Lewis et al. 1710* (MO), *2508* (DUKE, MO). Cerro Pilon, *Liesner 766* (DUKE, F, MO, NY, US, USF). Along road and in cloud forest

FIGURE 7. *Elateriopsis oerstedii* (Cogn.) Pittier. Habit (⅗). [After *Lewis et al.* 2508].

5 mi N of El Valle de Antón, *Luteyn 1192* (DUKE). El Valle de Antón and vicinity, *Maurice 772* (US); *Seibert 463* (MO). Penonomé and vicinity, *Williams 1156* (NY). COLÓN: Along the Río Guanche, *Croat 26154* (MO); *D'Arcy 9728* (MO); *Gentry 6311* (F, MO). 10 mi SW of Portobelo, 2–4 mi from coast, *Liesner 1101* (F, MO, NY, US, USF). N side of Río Guanche, ½ km upstream from Puerto Pilón-Portobelo Highway bridge, *Nee 7108* (MO). DARIÉN: Río Pirre and vicinity, *Croat & Porter 15500* (MO); *Duke 5071* (GH, MO, US), *5184* (GH, MO). Panamerican Highway between Pucro and Río Punusa, *Duke 5397* (GH, MO). Río Pirre and vicinity, *Gentry & Clewell 6934* (MO). Río Pucuro base camp, Río Pucuro between Cerro Mali and Cerro Tacarcuna, *Gentry & Mori 13875* (USF). Quebrada "Camachimuricate," *Kennedy 2846* (F, MO, NY, US). Paca, just below Caná, *Williams 800A* (NY). PANAMÁ: Upper Pequení between Salamanca Hydrographic station and Río Boqueron, *Allen 17285* (MO). Between Cañasas and Sabalo, *Duke 14455* (MO). Cerro Jefe, *Dwyer & Gentry 9057A* (MO). Tributary of Río Chagres, 5 mi SW of Cerro Brewster, *Lewis et al. 3472* (DUKE, MO), *3489* (MO). SAN BLAS: Río Chucunaque, 2–10 mi above Cuna-Darién boundary, *Duke 8561* (MO, US). Along headwaters of Río Mulatupo, *Elias 1788* (MO). VERAGUAS: Río Primero Braso, 2.5 km beyond Escuela Agrícola Alto Piedra near Santa Fé, *Croat 25522* (MO). Río Segundo Braso, 8 km beyond Escuela Agrícola Alto Piedra near Santa Fé, *Croat 25541* (MO). NW of Santa Fé, 8.8 km from Escuela Agrícola Alto de Piedra on road to Calovebora, *Mori 6654* (MO, USF). 11 km from Escuela Agrícola Alto de Piedra, in forest along Río dos Bocas, *Mori & Kallunki 3168* (MO, USF). NW of Santa Fé, 1.5 km from Escuela Agrícola Alto de Piedra, on school property S of school, *Mori & Kallunki 5329* (MO, USF). 6–7 km W of Santa Fé on new road past Agricultural School, *Nee 9745* (MO, USF).

8. FEVILLEA

Fevillea L., Sp. Pl. 1013. 1753; Gen. Pl., ed. 5. 443. 1754. LECTOTYPE: *F. cordifolia* L.

Nhandiroba Plum. ex Adans., Fam. Pl. 2: 139. 1763. TYPE: not designated.
Hypanthera Manso, Enum. Subst. Bras. 37. 1836. TYPE: *H. guapeva* Manso.

Dioecious, tendriled *vines* or *lianas*; stems 5-sulcate. *Leaves* petiolate, simple, entire, angulate or 3- or 5-lobate; tendrils 2-branched near the apex. *Staminate flowers* in axillary panicles; calyx campanulate, 5-lobate; corolla 5-lobate, spreading; stamens 5, free, the filaments recurving, the anthers 1-celled, straight. *Pistillate flowers* disposed as the staminate flowers; calyx and corolla as in the staminate flowers; ovary globose, 3-carpellate, the styles 3, connate for at least part of their length, the stigmas forming a capitate, 3-lobate head; staminodia minute, sometimes reduced to the glands, or absent. *Fruit* globose, indehiscent, with circumferential receptacle scar near the apex; seeds several in each carpel, pendulous, orbicular to elliptic, compressed, the testa rugose or somewhat echinate.

Fevillea is a genus of about seven species in the Neotropics. A single species occurs in Panama.

Literature:

Cogniaux, A. 1916. Cucurbitaceae: Fevilleae et Melothrieae *in* A. Engler. Das Pflanzenreich 88 (IV. Fam. 275, II): 1–277.

1. **Fevillea cordifolia** L., Sp. Pl. 1013. 1753; non Vell., 1827. TYPE: not known. —FIG. 8.

Trichosanthes punctata L., Amoen. Acad. 3: 423. 1756. TYPE: without locality, Herb. Linn. 11801 (LINN, not seen, microfiche MO).

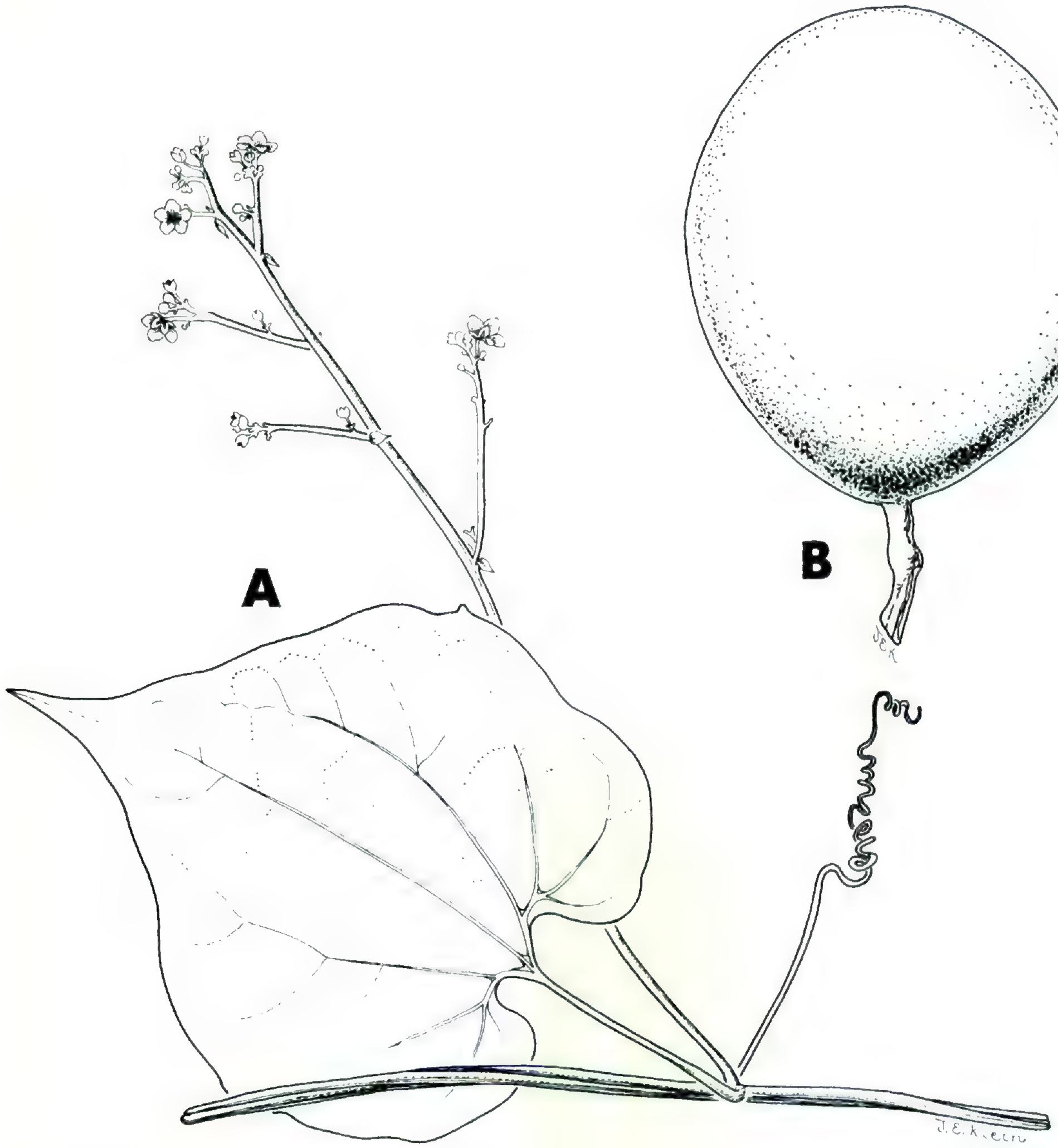


FIGURE 8. *Fevillea cordifolia* L. Habit (×7/10). [After *Croat* 22537].

Fevillea scandens L., Sp. Pl. ed. 2. 1457. 1763. TYPE: not known.
F. trilobata Reichard, Syst. Pl. 4: 253. 1780, non L., 1753. TYPE: not known.
F. punctata (L.) Poir. in Lam., Encycl. Méth. Bot. 4: 418. 1796.
F. hederacea Poir. in Lam., Encycl. Méth. Bot. 4: 419. 1796. TYPE: not known.
F. javilla H.B.K., Nov. Gen Sp. Pl. 2: 124. 1817. TYPE: not known.
Nhandiroba scandens (L.) Desc., Fl. Méd. Ant. 8: 66. 1829.
Fevillea cordifolia var. *hederacea* (Poir.) Cogn. in DC., Monogr. Phan. 3: 943. 1881.
Nhandiroba cordifolia (L.) Kuntze, Rev. Gen. 1: 257. 1891.

Lianas; stems, glabrous, often reddish. *Leaves* simple, cordate, 6–15 cm long, 4–12 cm wide, apex acuminate to attenuate, the base cordate, the margin with remote, rounded, glandular teeth, minutely ciliate, chartaceous to subcoriaceous, the upper and the lower surfaces minutely pustulate and usually somewhat puberulent on the veins; petiole 2–8 cm long, slender, striate; tendrils 2-branched

near the apex. *Staminate flowers* axillary, paniculate, the rachis 10–20 cm long, puberulent, each branch with a small, ovate bracteole at the base; pedicels 1–2 mm long, slender; calyx campanulate, greenish yellow, puberulent, ciliate, lobate to near the middle, the lobes broadly lanceolate, ca. 2 mm long, acute; corolla greenish yellow, the lobes broadly obovate, 3–4 mm long, the apex rounded, glabrous on the outer surface, puberulent toward the base on the inner surface, bearing a narrow flap of tissue on the lower ⅓ of petal separating 2 shallow nectary cups, weakly 7-nerved for most their length; stamens ca. 1 mm long, the anthers about as long as broad, equalling or longer than the filaments. *Pistillate flowers* disposed as the staminate flowers; calyx and corolla similar to the staminate flowers; ovary globose, 3–4 mm in diameter, puberulent, styles ca. 1 mm long, connate to near middle, the stigmas forming a capitate, 3-lobate head. *Fruits* green, flesh greenish white, globose or subglobose, 7–12 cm in diameter, the surface granular, a circumferential scar near the apex, indehiscent; seeds 6, 2 in each carpel, pendulous, lenticular, 5–6 cm long, 4–5 cm wide, ca. 1 cm thick, white, the testa punctate and minutely echinate.

Fevillea cordifolia ranges from Central America and the West Indies south to Peru and the Amazon basin of Brazil. It is uncommon in Panama, occurring in tropical moist forests, often climbing into the canopy.

CANAL ZONE: Barro Colorado Island, *Croat 11918* (DUKE, F, GH, MO, NY, USF). Coco Solo, *Gentry 6425* (MO). CHIRIQUÍ: Rabo de Puerco, 8 km W of Puerto Armuelles, Burica Peninsula, *Busey 440* (F, MO, NY, US, USF). Along Quanabana, Burica Peninsula, *Croat 22537* (MO, US). San Bartolomé, Burica Peninsula, *Woodson & Schery 872* (MO, NY, US). DARIÉN: Río Sabana above Santa Fé, *Duke 14107* (MO, NY). LOS SANTOS: Vicinity of Tonosí, *Duke 12484* (MO). 17.8 mi S of Macaracas, *Lewis et al. 1605* (MO). PANAMÁ: 12.4 km E of Cañita, *Witherspoon & Witherspoon 8704* (MO).

9. FRANTZIA

Frantzia Pittier, Contr. U.S. Natl. Herb. 13: 127. 1910. TYPE: *F. pittieri* (Cogn.) Pittier.

Polakowskia Pittier, Contr. U.S. Natl. Herb. 13: 131. 1910. TYPE: *P. tacaco* Pittier.

Monoecious, tendriled *vines*; stems 5- to 10-sulcate. *Leaves* petiolate, simple, entire or 5- to 5-lobate; tendrils 3- to 5-branched. *Staminate flowers* in axillary racemes or panicles; calyx rotate to urceolate, 5-lobate; corolla 5-lobate, the lobes spreading; stamens 5, the filaments connate, the anthers sessile, connate, flexuous, forming an irregular head; nectaries 10, forming a depressed spherical cushion at the base of the staminal column or pouchlike and sunken into the bottom of the hypanthium and protruding on the underside of the calyx. *Pistillate flowers* solitary or few in the same axils as the staminate flowers; calyx and corolla as in the staminate flowers; ovary fusiform, 1-carpellate, the single ovule pendulous; styles 5, connate, erect, the stigmas 5, forming a peltate, 5-lobate head; nectaries as in the staminate flowers. *Fruits* ovate to fusiform, indehiscent or 2-valvate, with or without spines, firm and fibrous; seed ovate to elliptic, compressed, the testa smooth.

Frantzia embraces five species, three endemic to Costa Rica, one endemic to Panama, and the other occurring in both countries. The genus is divided into

two sections, sect. *Frantzia* and sect. *Polakowskia* on the basis of nectary structure. The two Panamanian species are both placed in sect. *Frantzia*.

Literature:

Pittier, H. 1910. New or noteworthy plants from Colombia and Central America—II. Contr. U.S. Natl. Herb. 13: 93–132.

Wunderlin, R. P. 1976. Two new species and a new combination in *Frantzia* (Cucurbitaceae). Brittonia 28: 239–244.

———. 1977. A new species of *Frantzia* (Cucurbitaceae) from Panama. Bull. Torrey Bot. Club 104: 102–104.

a. Inflorescences long pedunculate, subcapitate clusters ..... 1. *F. panamensis*
aa. Inflorescences racemose paniculate ..... 2. *F. pittieri*

1. **Frantzia panamensis** Wunderlin, Bull. Torrey Bot. Club 104: 102. 1977. TYPE: Panama, *Davidson 416* (F).

Vines; stems glabrous. *Leaves* simple, blade lanceolate, 8–12 cm long, 5–7 cm wide, the apex acuminate, the base deeply cordate, the margin coarsely dentate, chartaceous, the upper surface minutely scabrous pustulate, scabrous puberulent on the principal veins, the lower surface scabrous puberulent on veins, the petiole 2.0–3.5 cm long, glabrous, sulcate; tendrils 5-branched, usually only 1–3 branches well developed, glabrous. *Staminate flowers* axillary, long pedunculate in subcapitate clusters; peduncle 6–8 cm long, slender, glabrous; pedicels filiform, 6–8 mm long, tomentellous; calyx depressed urceolate, tomentose, 3–4 mm long, 6–8 mm wide, green, the lobes setose, 3–4 mm long; corolla lobes broadly lanceolate to triangular, 7–9 mm long, ca. 6 mm wide at the base, the apex acute, connate for ca. 2 mm at the base, spreading, greenish white, 7- to 11-nerved, the outer surface tomentose, the inner surface sparsely stipitate glandular; staminal column ca. 3 mm long, the anthers forming an irregular head ca. 3 mm in diameter, spreading after maturity; nectaries forming a depressed spherical cushion at the base of the staminal column, each opening by a horizontal pore at the periphery. *Pistillate flowers* solitary, axillary; peduncle 6–8 mm long, glabrate; calyx tomentellous, otherwise as in the staminate flowers; corolla as in the staminate; nectaries, the style and stigma not seen; ovary broadly fusiform, ca. 13 mm long, ca. 6 mm in diameter, tomentose, aculeate on the lower half. *Fruits* unknown, but probably similar to the following species.

This species is known only from the type and the following collection.

CHIRIQUÍ: Top of peak between Baru and Respinga, *D'Arcy 10135* (MO). Without other locality, *Davidson 416* (F).

2. **Frantzia pittieri** (Cogn.) Pittier, Contr. U.S. Natl. Herb. 13: 139. 1910.—FIG. 9.

Cyclanthera pittieri Cogn., Bull. Soc. Roy. Belg. 30: 275. 1891. TYPE: Costa Rica, *Tonduz 2511* (US, isotype).

C. pittieri var. *quinqueloba* Cogn., Bull. Soc. Roy. Bot. Belgique 30: 276. 1910. TYPE: Costa Rica, *Pittier 3506* (BR, not seen).

Frantzia montana Pittier, Contr., U.S. Natl. Herb. 13: 128. 1910. TYPE: Costa Rica, *Pittier 13192* (US, holotype).

FIGURE 9. *Frantzia pittieri* (Cogn.) Pittier. Habit (×7/10). [After *Hladik 179*].

F. pittieri var. *quinqueloba* (Cogn.) Pittier, Contr. U.S. Natl. Herb. 30: 276. 1910.
Elateriopsis pittieri (Cogn.) Cuf., Archivo Bot. 10: 50. 1934.

Vines; stems slender, glabrous or puberulent. *Leaves* simple, blade (5–)10–15(–20) cm long, (5–)10–15(–20) cm wide, broadly ovate to suborbicular in outline; entire or 3- to 5-lobate, apically acuminate, basally cordate, the margin glandularly dentate, chartaceous, the upper surface scabrous with pustular-based trichomes, the lower surface glabrous or tomentellous at the base and on the main veins; petiole 3–8(–15) cm long, slender, striate; tendrils 3- to 5-branched. *Staminate flowers* axillary, racemose paniculate, rarely becoming distinctly paniculate; rachis 10–25 cm long, slender, flowered for most its length, the flowers in 6–15 umbelloid clusters; pedicels 5–20 mm long, filiform; calyx rotate to campanulate, 1–2 mm long, green, lobes ca. 1 mm long, subulate to triangular; corolla ca. 1 cm in diameter, greenish white, the lobes 3–5 mm long, 2–4 mm wide at the base, triangular to lanceolate, the outer surface glabrous, the inner

surface puberulent toward the base, 7- to 9-ribbed; staminal column 2–3 mm long, the anthers forming an irregular head; nectaries forming a depressed spherical cushion at the base of the staminal column, each opening by a pore on the periphery. *Pistillate flowers* solitary in the same axils as the staminate flowers; calyx and corolla as in staminate, but slightly smaller; ovary fusiform, 3–4 mm long, usually setose toward the base, rarely setose on the entire surface, styles ca. 1 mm long, the stigma capitate, ca. 2 mm in diameter; nectaries as in the staminate flowers, but the openings slightly larger. *Fruit* green with white or light green spots, 4–6 cm long, 3–4 cm in diameter, ovate to fusiform, the surface slightly rugose, shallow pitted, usually spiny, at least near the base, rarely spineless, frequently 10-sulcate, woody and fibrous, indehiscent; seed solitary, 2–3 cm long, 1–2 cm wide, 4–5 mm thick, ovate to elliptic, the testa smooth.

This is a variable species occurring in forest margins and thickets in Panama from 1,400 to 2,700 m. It is also found in Costa Rica down to 100 m.

BOCAS DEL TORO: Water Valley, Chiriquí Lagoon, *Wedel 763* (GH, MO, US), *1128* (GH, MO), *1443*, *1457*, *1522*, *1662* (all GH, MO, US). Pumpkin River, Chiriquí Lagoon, *Wedel 2590* (GH, MO, US). Nievecita, *Woodson & Schery 1026* (MO, NY, US); *Woodson et al. 1841* (MO). CHIRIQUÍ: Trail from Cerro Punta to headwaters of Río Caldera, *Allen 1443* (F, GH, MO, NY). Cerro Punta, *Blum et al. 2434* (FSU, MO). Camino que va desde el pueblo de Cerro Punta a la zona maderera de Las Nubes, *Correa 1322* (MO). Between Bambito and Cerro Punta, *Croat 10598* (DUKE, F, MO, NY). Methodist camp near Nueva Swissa and Cerro Punta, *Croat 13533* (GH, MO), *Croat 26290* (MO). Above Boquete on road to Cerro Horquita, *Croat 27030* (MO). Above Río San Félix near town of San Félix, ca. 13 mi N of Río San Félix bridge, *Croat 33450* (MO, USF). NW side of Cerro Punta between Monte Lirio and El Hato de Volcán, *Croat & Porter 15949* (MO, NY). Alto Respinga and above, *D'Arcy 9984* (MO). Cerro Respinga, E of Cerro Punta, *D'Arcy & D'Arcy 6536* (F, MO). E slope of Volcán de Chiriquí (Baru) WNW of Boquete, *Davidse & D'Arcy 10144* (MO). Río Chiriquí Viejo valley, *Duke 9021* (USF). Cerro Horquete, NW of Boquete, *Duke et al. 13641* (DUKE, MO). Cerro Horquete, NW of Boquete, *Duke et al. 13641* (DUKE, MO); *Dwyer et al. 463* (F, GH, MO, NY, US). Boquete, Fred Collins Finca, *Ebinger 696* (M, MO, US, USF). Cerro Respinga, E of Cerro Punta, *Gentry 5938* (F, MO, NY). 1.4 mi S of Cerro Punta, *Graham 294* (GH, MICH). Bojo Boquete, *Hladik 179* (MO). Cerro Horqueta, NW of Boquete, *Maurice 889* (F, MO, US). Cerro Punta, 2.5 km SE of town, *Mori & Kallunki 5636* (MO, USF). N of San Félix at Chiriquí-Bocas del Toro border on Cerro Colorado copper mine road, *Mori & Kallunki 5969* (USF). Bajo Grande, 1–3 km E of town of Cerro Punta, *Nee 10005* (USF). Around camp aquacatal, E slope of Chiriquí Volcano, *Pittier 3081* (GH, US). Cerro Punta, *Ridgeway & Solis 2387* (GH, MO); *Tyson 1032* (FSU). Bambito, 1 mi SW of Cerro Punta, *Tyson 5659* (FSU, MO). On mountains above Bambito, 1 mi S of Cerro Punta, *Tyson 5770* (FSU). Cerro Punta, *Tyson 5795* (FSU, MO). Río Chiriquí Viejo valley, *White 163* (F, MO). Cerro Punta, *White 201* (F, MO, US). Streamside near Nueva Suiza and ca. 2 mi E of Cerro Punta, *Wilbur et al. 13011* (DUKE). Wooded slopes ca. 1 km N of Las Nubes, E of Cerro Punta and 5 km NW of Cerro Punta town, 2000–2300 m, *Wilbur et al. 15223* (DUKE). Casita Alta, Volcán de Chiriquí, *Woodson et al. 920* (F, GH, MO, NY). VERAGUAS: Above Santa Fé beyond Escuela Agrícola Interamericana, 1.8 mi beyond fork in road on Pacific slope, *Croat 34183* (MO). NW of Santa Fé, 1 km from Escuela Agrícola Alto de Piedra, *Mori & Kallunki 4880* (USF). 6–7 km W of Santa Fé on new road past agriculture school, *Nee 9776* (USF).

10. GURANIA

Gurania (Schlecht.) Cogn., Bull. Soc. Roy. Bot. Belgique 14: 239. 1875.

Anguria sect. *Gurania* Schlecht., Linnaea 24: 789. 1851.

Dioecious, rarely monoecious, tendriled *vines* or *lianas*; stems 5- to 10-sulcate. *Leaves* petiolate, simple, entire, lobate, or 3- to 5-foliolate; tendrils simple.

Staminate flowers axillary, in racemes, or umbelloid heads; calyx tubular, 5-lobate; corolla 5-lobate, the lobes erect or only spreading; stamens 2, sessile or subsessile, free, attached to the hypanthium wall, the anthers straight or replicate. *Pistillate flowers* in axillary, fascicles, racemes, umbelloid heads, or flowers solitary; calyx and corolla similar to the staminate flowers; ovary oblong, 3-carpellate, the ovules numerous, horizontal, the styles 2, connate, erect, the stigmas 2. *Fruits* oblong to fusiform, cylindrical, indehiscent; seeds elliptic ovate, compressed.

Gurania is a genus of about 75 tropical species with four occurring in Panama. The genus is closely related to *Psiguria* and may not be distinct from it.

a. Calyx lobes much shorter than hypanthium tube; staminate inflorescences usually produced at nodal region on old leafless, woody stems ..... 4. *G. megistantha*
aa. Calyx lobes equalling or much longer than hypanthium tube; staminate inflorescences produced on leafy, herbaceous stems.
  b. Staminate flowers distinctly pedicellate; calyx lobes narrowly lanceolate; leaves usually 3-foliolate, rarely entire or 2- to 3-lobate ..... 1. *G. coccinea*
  bb. Staminate flowers sessile or subsessile; calyx lobes filiform; leaves 3- to 7-lobate.
    c. Corolla lobes subequalling calyx lobes; inflorescence pilose setose ..... 2. *G. eriantha*
    cc. Corolla lobes less than ½ the length of the calyx lobes; inflorescence pilose to pubescent ..... 3. *G. makoyana*

1. **Gurania coccinea** Cogn., Mém. Couronnés Mém. Acad. Roy. Sci. Belgique 27: 42. 1876. TYPE: Panama, *Fendler 125* (K, holotype, not seen; MO, US, isotypes).—FIG. 10.

Dioecious *vine*; stems 5- to 10-sulcate, pilose, rarely glabrate. *Leaves* usually 3-foliolate, sometimes simple and entire, 2- to 3-lobate, or imperfectly foliolate, the leaflets sessile or with petiolules to 15 mm long, 12–18 cm long, 5–8 cm wide, the terminal leaflet elliptic or narrowly obovate, the lateral leaflets obliquely ovate, often with a pronounced basal lobe on the outer margin, the apex acute to acuminate, the base cuneate, the margin denticulate, chartaceous, the upper and the lower surfaces pilose, especially on the veins, rarely glabrate; petioles 2–6 cm long, pilose, rarely glabrate; tendrils simple, sparsely pilose or glabrate. *Staminate flowers* in axillary, usually long pedunculate, umbelloid racemes, the rachis pilose to rarely glabrate; peduncles to 20 cm long; pedicels 4–15 mm long; calyx orange, tubular with a bulbous base, the outer surface pilose, the inner surface papillose puberulent, lobed for ⅓–½ its length, the lobes lanceolate, spreading; corolla yellow, slightly exceeding the calyx, the lobes lanceolate, densely papillose on both the surfaces; anthers 2, free, attached to the hypanthium wall, subsessile, the anthers ovate oblong, replicate at the base, ca. 3 mm long, appendix ca. 2 mm long, slightly papillose. *Pistillate flowers* several at leafless nodes on the upper part of the stem; calyx and corolla as in the staminate flowers, but glabrous on the inner surface; ovary linear fusiform, ca. 1.5 cm long, the rachis pilose to glabrate, ovules numerous, horizontal, the styles 2, connate, short, stout, stigmas 2, bifid, the inner surface papillose and grooved, much longer than the stylar column. *Fruits* pale green with light spots, 4–6 cm long, 1.5–2.5 cm in diameter, longitudinally grooved, the old flowers sometimes persisting; seeds white, elliptic ovoid, compressed, 6–9 mm long, 3–4 mm wide, the testa rugulose.

FIGURE 10. *Gurania*.—A. B. *G. coccinea* (Cogn.) Pittier.—A. Habit (×1). [After *Blum & Duke 2198*].—B. Immature fruit (×⅗). [After *Croat 14577*].—C. *G. megistantha* Donn. Sm. Stem and inflorescence (×⅗). [After *Gentry 4909*].

This species is known from the tropical wet forest at elevations up to 1,000 m. It is reported only from Panama, but is to be expected in Costa Rica on the Atlantic side. The native name is "ya-te-vi" or "bien te veo."

This and one, or perhaps two, other *Gurania* species are said to be much

feared by some of the natives. It is said to cause an itching and blistering or ulcering of the skin, sometimes accompanied with swelling or a fever or nausea. Various accounts attribute the plant hairs, a fly or bug which is harbored in the flowers, or a large caterpillar which feeds on the leaves. Contemporary botanists report collecting this and other *Gurania* species without any ill effects.

This and at least some other *Gurania* species are pollinated by various species of heliconid butterflies.

BOCAS DEL TORO: Fish Creek Mountains, Chiriquí Lagoon, *Wedel 2251* (MO). CANAL ZONE: Chagres, *Fendler 125* (MO, US). Woods near Gatún Station, *Hayes 134* (NY). Militar Reserva Fuerte Sherman between Gatún and Piña, *Liesner 1334* (DUKE, F, MO, NY, US, USF). Hills around the Aqua Clara Reservoir near Gatún, *Pittier 2657* (US). Forest along the Río Indio de Gatún, *Pittier 2787* (GH). Hills N of Frijoles, *Standley 27422* (US). BARRO COLORADO ISLAND: *Croat 14077, 14577* (both MO); *Foster 2039* (DUKE); *Frost 229* (F); *Shattuck 641* (F, GH, MO); *Wetmore et al. 50* (F, GH). COCLÉ: Hills N of El Valle de Antón, *Allen 2346* (MO). Foothills of Cerro Pilón, above El Valle de Antón, *Correa & Duke 14667* (MO); *Croat 14077* (MO, NY), *14328* (MO). El Valle de Antón, *Lewis et al. 2536* (MO). Along road ca. 8 mi N of El Valle de Antón, *Luteyn & Kennedy 1682* (DUKE). Foot of Cerro Pilon, above El Valle de Antón, *Porter et al. 4420A* (MO). COLÓN: Santa Rita Ridge, *Dwyer & Gentry 3411* (MO). Santa Rita Ridge, ca. 4–5.5 mi E of Transisthmian Highway, *Lewis et al. 5292* (MO). LOS SANTOS: Cerro Pilón, *Dwyer 8621* (MO). PANAMÁ: Cerro Jefe, *Blum & Duke 2198* (FSU, MO). Santa Rita Trail, *Cowell 129* (NY). Cerro Jefe, 4.6 km beyond peak on road to Altos de Pacora, 26.3 km from Interamerican Highway, *Croat 35910* (MO). Cerro Campana, *Duke 10727* (MO). Cerro Jefe, *Duke 15244* (MO). Cerro Campana, *Gentry 4916* (MO). Campo Tres, 3 mi NE of Altos de Pacora, *Liesner 511* (DUKE, F, MO, NY, US, USF). Cerro Campana, 8.6 mi SW of Capira, *Luteyn 1033* (DUKE, F). Summit of Cerro Campana, *Porter et al. 4886* (MO). SAN BLAS: Permé, *Cooper 243* (NY). SE of Puerto Obaldía, *Croat 16755* (MO). VERAGUAS: Río Segundo Brasso, 8 km beyond Escuela Agrícola Alto Piedra beyond Santa Fé, *Croat 25561* (MO). Valley of Río Dos Bocas along road between Escuela Agrícola Alto Piedra and Calovébora, 15.6 km NW of Santa Fé, *Croat 27603* (MO). 0.2 mi beyond fork in road at Escuela Agrícola Alto Piedra on road to Río Calovébora, *Croat & Folsom 33883* (MO, USF). NW of Santa Fé, 8.8 km from Escuela Agrícola Alto de Piedra, *Mori & Kallunki 3985* (MO). Lower montane wet forest 6–7 km W of Santa Fé on new road past agriculture school, *Nee 9736, 11254* (both MO, USF). Cutover slopes N of the government agricultural camp ca. 2 km N of Santa Fé towards the continental divide, *Wilbur & Luteyn 19105* (DUKE). Along first branch of Río Santa Maria on road from Santa Fé, *Witherspoon & Dressler 8915* (MO, USF).

2. **Gurania eriantha** (Poepp. & Endl.) Cogn., Mém. Couronnés Mém. Acad. Roy. Sci. Belgique 27: 16. 1876.

Anguria eriantha Poepp. & Endl., Nov. Gen. Sp. Pl. 2: 52. 1838. TYPE: Peru, *Weberbauer 2330* (W, holotype, not seen; MO, photo of isotype at B, specimen now destroyed).

A. speciosa Poepp. & Endl., Nov. Gen. Sp. Pl. 2: 51. 1838. TYPE: not known.

Gurania speciosa (Poepp. & Endl.) Cogn., Mém. Couronnés Mém. Acad. Roy. Sci. Belgique 27: 16. 1876.

G. martiana Cogn., Mém. Couronnés Mém. Acad. Roy. Sci. Belgique 27: 16. 1876. TYPE: not known.

G. hirsuta Cogn., Bot. Jahrb. Syst. 23: 134. 1896. TYPE: BR, holotype, not seen; MO, photo of isotype at B, specimen now destroyed).

G. andreana Cogn., Bull. Soc. Roy. Bot. Belgique, sér. 2. 49: 390. 1904. TYPE: not known.

Dioecious, tendriled *vines*; stems 5- to 10-sulcate, pilose. *Leaves* simple, blade ovate to suborbicular, entire or 3- to 5-lobate, 10–25 cm long, nearly as wide as long, the apex acuminate to caudate, the base cordate, the margin denticulate, submembranaceous to chartaceous, the upper surface minutely pustulate, the upper and the lower surfaces pilose; petioles 2–6 cm long, slender, striate, pilose; tendrils, simple, pilose. *Staminate flowers* in axillary, usually long pedunculate,

capituliform racemes, the rachis densely pilose; peduncles to 40 cm long; flowers sessile or subsessile; calyx orange, urceolate, the outer surface pilose, the inner surface glabrous, lobes ca. 1.5 cm long, filiform, erect or slightly spreading, pilose on the outer surface; corolla yellow, the lobes equalling or slightly longer than the calyx lobes, filiform, densely papillose puberulent on both the surfaces; stamens 2, attached to the hypanthium wall, subsessile, the anthers ovate subrectangular, 2.5–3.0 mm long, replicate at both ends, without appendix. *Pistillate flowers* solitary or several at the leafless nodes on the upper part of the stem; calyx and corolla as in the staminate flowers but glabrous on the inner surfaces; ovary elliptical, pilose, ovules numerous, horizontal, the styles 2, connate, thick, the stigmas 2, emarginate at the apex, the inner surface papillose and medially grooved, subequalling the style column. *Fruit* oblong, pilose, 3.5–4.5 cm long, 2.5–3.0 cm in diameter, the old flowers persisting; seeds numerous, light brown, elliptical, compressed, 10–12 mm long, 5–6 mm wide, the margin somewhat thickened, the testa roughened.

Specimens have been seen from Peru, Panama, and Costa Rica with only a single collection from the latter two countries. The species occurs in tropical wet forests at low elevations. The native name in Peru for this species is "usiya-o."

DARIÉN: La Boca de Pirre, *Bristan 1250* (MO, NY).

3. **Gurania makoyana** (Lem.) Cogn., Mém. Couronnés Mém. Acad. Roy. Sci. Belgique 27: 17. 1876.

Anguria makoyana Lem., Fl. Serres Jard. Eur. 3: *tab.* 222. 1847. TYPE: Described from plants cultivated in Belgium from seeds said to come from Guatemala (BR, not seen).
Gurania seemaniana Cogn., Mém. Couronnés Mém. Acad. Roy. Sci. Belgique 27: 35. 1876. TYPE: Panama (BR, not seen).
G. donnell-smithii Cogn. in Donnell Smith, Bot. Gaz. (Crawfordsville) 16: 10. 1891. TYPE: Guatemala, *Donnell-Smith 1511* (BR, holotype, not seen; US, isotype).

Dioecious *vines*; stems 5- to 10-sulcate, pilose, pubescent, or villous. *Leaves* simple, the blade broadly ovate to suborbicular in outline, shallowly to deeply 3- to 7-lobate, the juvenile leaves often entire or shallowly lobed, 15–30(–40) cm long, nearly as wide as long, the apex acuminate, the base cordate, the margin denticulate, chartaceous, the upper surface minutely pustulate, the upper and the lower surfaces pilose, or villous, especially on the veins; petioles 4–10 cm long, slender, striate, pilose, pubescent, or villous; tendrils simple, pilose, pubescent, or glabrate. *Staminate flowers* in axillary, usually long pedunculate, capituliform racemes, pilose, villous, or pubescent; peduncles to 30 cm long; flowers sessile or subsessile; calyx orange, urceolate, the outer surface pilose or pubescent, the inner surface papillose puberulent, the lobes ca. 2 cm long, filiform, erect or slightly spreading, pilose on the outer surface; corolla yellow, about ⅓ the length of the calyx lobes, the lobes lanceolate, densely papillose puberulent on both the surfaces; anthers 2, free, attached to the hypanthium wall, subsessile, the anther lanceolate, replicate at the base, ca. 6 mm long, the appendix ca. 1 mm long, smooth. *Pistillate flowers* solitary or several at leafless nodes on the upper part of the stem; calyx and corollas as in the staminate flowers, but glabrous on the inner surfaces; ovary linear fusiform, ca. 1.5 cm long, pilose to

glabrate, the ovules numerous, horizontal, the styles 2, connate, thick, the stigmas 2, emarginate at the apex, the inner surface papillose and grooved down the center, equalling the style column in length. *Fruits* green, cylindric fusiform, 4–6 cm long, 2.0–2.5 cm in diameter, glabrate, the old flowers persisting; seeds numerous, white, elliptic ovate, compressed, 6–9 mm long, 3–5 mm wide, the testa rugulose.

A highly variable species, which along with several other Central and South American species, is in need of further study. *Gurania levyana* Cogn. has been reported from Panama by Cogniaux (1916) and Standley (1928). All Panamanian specimens identified as this species by these and other workers and seen by me have been referred to *G. makoyana*. Typical *G. levyana* appears to be restricted to South America.

Gurania makoyana occurs in open tropical moist forests and clearings at elevations up to 1,000 m. It ranges from Guatemala to Panama and perhaps into South America.

This species is known locally as "ya-te-vi" (as is *G. coccinea*), "bejuco picado," "Chibigui juncara," or "bejuco ya te vi." It reportedly has the same irritating characteristics as *G. coccinea* as discussed under that species.

BOCAS DEL TORO: Region of Almirante, Buena Vista, *Cooper 229*. Railroad station at Milla 7.5, *Croat & Porter 16409* (MO). Río Teribe, *Duke & Kirkbride 418* (MO). Changuinola Valley, *Dunlap s.n.* (F). Farm 6, Changuinola Valley, *Dunlap 491* (F, US). Out Zigla Road at junction of Changuinola and Tuibe Rivers, *Lazor et al. 2555* (FSU). Punta Róbalo to Río Róbalo, *Seibert 1565* (MO, US). Chiriquí Lagoon, *Wedel s.n.* (MO). Water valley, Chiriquí Lagoon, *Wedel 1594* (GH, MO, US). CANAL ZONE: Mojinga Swamp near mouth of Río Chagres, *Allen 905* (MO). Pipeline road near Gamboa, *Clewell & Tyson 3246* (MO); *Croat 4686* (MO). E side of Pena Blanco Peninsula, *Croat 5385* (MO). Radar Station Road, 1 mi N of Summit Gardens, *Croat 9077* (MO, NY). Pipeline road near Gamboa, *Croat 9358* (MO, SCZ). Radar Station Road, 1 mi N of Summit Gardens, *Croat 14253* (MO, USF). Road K-10, 1–2 mi from Kobbe Arraiján Highway, *Duke 11723, 11724* (both MO). Chagres, *Fendler 124* (MO), *126* (GH, MO). Changares, Isthmus of Panama, *Fendler 126* (US). Woods near Gatún Station, *Hayes 135* (NY). Former town of Empire, *Hunter & Allen 778* (GH, MO). Limbo Gun Club, MARU station, *Lazor & Tyson 3466* (FSU). Madden Forest Preserve, *Lewis et al. 5038* (MO). Hilly forest around Agua Clara Reservoir, near Gatún, *Maxon 4648* (F, US). 9 km NW of Gamboa on Pipeline Road, *Nee 6635* (MO). Towers on Loma la Toba, 3 km SW of mouth of Chagres River, *Nee 8939* (MO, USF). Road S1, 4 km W of Gatún Dam, *Nee & Hale 9689* (MO, USF). Near old Fort Lorenzo, *Piper 5901* (US). Navy Reservation N of Gamboa, *Robyns 65-46* (MO). BARRO COLORADO ISLAND: *Aviles 87B* (MO); *Croat 5674, 8593* (both MO); *D'Arcy 3904* (MO); *Frost 215* (F); *Shattuck 110* (MO), *601* (F, MO, US); *Standley 31249* (US); *Wetmore & Woodworth 16* (GH); *Wilson 38* (F, MO); *Woodworth & Vestel 713* (F, GH, MO). CHIRIQUÍ: San Bartolomé, *Woodson & Schery 912* (MO). COCLÉ: El Valle de Antón, *Allen 1653, 1832* (both MO). La Mesa above El Valle de Antón, *Croat 14308, 14389* (both MO). Cerro Pilón above El Valle de Antón, *Croat 22926* (DUKE, MO); *Duke & Lallathin 15015* (MO). La Mesa above El Valle de Antón, *Gentry 6831* (MO, USF); *Hladik 333* (MO); *Kennedy et al. 3031* (F, MO, NY, US). El Valle de Antón, *Kirkbride 1085* (MO). In rain forest on Caracoral below the elfin forest, *Kirkbride A1113* (MO). El Valle de Antón, *Lewis et al. 1763* (GH, MO, US). Foot of Cerro Pilón, *Porter et al. 4420* (MO). Bismark above Penonomé, *Williams 315* (NY, US). COLÓN: Santa Rita Ridge, *Correa & Dressler 678* (DUKE, FSU, GH, MO). Al este de la zona montanosa de Santa Rita, *Correa & Dressler 937* (MO). Santa Rita Ridge, along river near Guasima, *Croat 9943* (MO). Santa Rita Ridge, *Croat 13852* (F, MO), *14186* (MO). Santa Rita Ridge, *Croat & Porter 15608* (MO). Santa Rita Ridge, *Dwyer & Gentry 9344* (MO); *Gentry 6570* (F, MO). Santa Rita Ridge, *Lazor & Tyson 3024* (FSU). Santa Rita Ridge, *Lewis et al. 5264* (MO). Santa Rita Ridge, 1 mi SW of Portobelo, 2–4 mi from coast, *Liesner 1062* (MO). Forests around Portobelo, *Maxon 5799* (F, US). DARIÉN: Río Tuquesa below

Quebrada Venado, *Bristan 1085* (MO). 2–3 mi SE of El Real, *Duke 4839* (GH, MO). Road from El Real to Pinogana, *Duke 5148* (MO). Loma Piriaque, *Duke 8101* (MO). Río Morti, ca. 6 mi upstream from Mortí Abajo, *Duke 10149* (MO). 1–4 mi N of Pucro, *Duke 13009* (MO). Trail from Río Pucro to Quebrada Maskia, *Duke 13073* (MO). Río Uruti, *Duke & Bristan 230* (MO). Río Pirre, old forest 10 mi S of El Real near "Dos Bocas," *Foster & Lowenbach 2266* (DUKE, MO). Slopes of Cerro Chucula, drainage of Río Pavarondo, *Gentry 4252* (MO). Río Pirre, *Kennedy 2902* (F, MO, US). Between Mannene and the mouth of the Río Cuasí, *Kirkbride & Bristan 1534* (MO). Upper Río Tuquesa, *Le Clezia 149* (MO). Along the Sambú River, *Pittier 5691* (US). Vicinity of Yaviza, along Panamerican Highway between Pinogana and Yaviza, 1 km from Tuira, *Stern et al. 134* (GH, MO, US). Caná-Cuasí Trail, *Terry & Terry 1491* (F, MO). Caná and vicinity, *Williams 801* (NY). PANAMÁ: Cerro Azul, near Goofy Lake, *Croat 11576* (MO). Cerro Campana above Su Lin Motel, *Croat 14762* (MO). Isla Alto de Majé (of Gorgas Memorial Laboratory) in the newly formed Lake of the Bayano River, *Croat 34376* (MO). Cerro Jefe, *Dwyer 8481* (MO). Cerro Azul, near Goofy Lake, *Ebinger 979* (MO). Cerro Jefe, *Gomez-Pompa et al. 3076* (MO). Santa Rita, *Gomez-Pompa et al. 3218* (MO). 2–3 mi S of Goofy Lake, road to Cerro Jefe, *Lewis et al. 235* (MO). Campo Tres, 3 mi NE of Altos de Pacora, *Liesner 550* (MO). 11 km from junction with Panamerican Highway, El Llano-Cartí Road, *Mori & Kallunki 3062* (MO, USF). 5–10 km NE of Altos de Pacora, ca. 15 km from Cerro Azul, *Mori et al. 4223* (MO, USF). El Llano-Cartí Road, 17.5 km from Panamerican Highway, *Mori et al. 4601* (MO, USF). Around Alhajuela, Chagres Valley, *Pittier 3489* (US). Cerro Azul, *Porter et al. 4085* (MO). Cerro Campana, above Su Lin Motel, *Porter et al. 4191* (MO). Villa Rosario, *Saldana 7* (MO). Juan Diaz, *Standley 30627* (US). Cerro Jefe, *Tyson 3401* (MO, SCZ). Cermeño, *Varela 7* (MO). SAN BLAS: Beach E of Puerto Obaldía, *Croat 16917* (MO). Mainland opposite Ailigandí, from mouth of Río Ailigandí to 2.5 mi inland, *Lewis et al. 162* (MO). Río Ailigandí, *Duke 10836* (MO). Forests around Puerto Obaldía, *Pittier 4333* (US). On trail between Río Diaz and Río Ailigandí, *Warner 228* (MO). VERAGUAS: Above Santa Fé beyond Escuela Agrícola Interamericana, 1.8 mi beyond fork in road on Pacific slope, *Croat 34169* (MO). 0.2 mi beyond fork in road at Escuela Agrícola Alto Piedra on road to Río Calovébora, *Croat & Folsom 33904* (MO). Above Río Primero Brazo 5 mi NW of Santa Fé, *Liesner 828* (MO, US). 5 mi W of Santa Fé on road past Escuela Agrícola Alto Piedra, *Liesner 912* (MO, USF). 6–7 km W of Santa Fé on new road past agriculture school, *Nee 9730* (MO). 3–4 km by road W of Santa Fé, *Nee 11279* (MO).

4. **Gurania megistantha** Donnell Smith, Bot. Gaz. (Crawfordsville) 33: 251. 1902. TYPE: Costa Rica, *Smith 6649* (US, holotype).

G. suberosa Standley, J. Wash. Acad. Sci. 15: 461. 1925. TYPE: Panama, *Standley 31461* (US, holotype).

Dioecious, tendriled *lianas*; juvenile stems 5- to 10-sulcate, pilose, older stems woody, with thick, ridged, corky periderm. *Leaves* simple, broadly ovate to suborbicular, shallowly to deeply 3-lobate, rarely 5-lobate or entire, 10–25 cm long, 9–20 cm wide, the apex acuminate, the base cordate, the margin minutely and remotely denticulate, chartaceous, the upper surface minutely pustulate, the upper and the lower surfaces pilose, especially on the veins; petioles 4–11 cm long, slender, striate, pilose, the tendrils simple, pilose or glabrate. *Staminate flowers* in sessile or subsessile, umbelloid racemes at the nodal regions on the old leafless stems, less commonly on short herbaceous branches arising from the old wood or the young stems, the rachis strigose, puberulent, or glabrate; peduncles 1–2 (–12) cm long; pedicels 1–3 cm long; calyx orange, tubular with a bulbous base, 1.5–3.5 cm long, the outer surface puberulent or glabrate, the inner surface densely papillose puberulent, lobed up to ca. ¼ its length, the lobes linear, spreading; corolla yellow, equalling or slightly exceeding the calyx, the lobes lanceolate, acute, densely papillose puberulent on both the surfaces; stamens 2, free, attached to the hypanthium wall, subsessile, the anthers linear ca. 2 cm

long, replicate at the base, the appendix linear triangulate, papillose, 8–10 cm long. *Pistillate flowers* in sessile or subsessile, umbelloid racemes on leafless branches on the upper part of the stem; calyx and corolla as in the staminate flowers; ovary oblong, glabrate, ovules numerous, horizontal, the styles 2, connate, thick, the stigmas 2, linear lanceolate, the inner surface papillose puberulent and medially grooved, ca. ½ the length of the style column. *Fruits* borne in tight clusters, pale green with light spots, elliptic 4–5 cm long, 1.5–2 cm wide, longitudinally grooved, old flowers persisting; seeds white, elliptic ovoid, compressed, 6–9 mm long, 3–4 mm wide, the testa rugulose.

Gurania megistantha is a species of tropical wet forest at elevations up to 1,000 m. It is also known from Costa Rica. The bright orange staminate flowers, with a long tubular hypanthium and short calyx lobes, usually borne on woody, corky, naked branches, make this one of the easiest of the Panamanian *Gurania* species to identify.

BOCAS DEL TORO: Region of Almirante, Buena Vista, *Cooper 215* (F). Quebrado Huron, *Kirkbride & Duke 423* (MO). Fish Creek Mountains, Chiriquí Lagoon, *Wedel 2202* (GH, MO), *2297* (MO), *2372* (GH, MO, US). CANAL ZONE: Mojinga Swamp near mouth of Río Chagres, *Allen 906* (GH, MO, NY). Telephone trail between Río Indio Hydrographic Station and the natural bridge of Río Puente, *Dodge & Allen 17477* (MO). Río Providencia, 3 km SE of Achiote near W border of Canal Zone, *Gentry & Nee 8671* (MO, USF). Río Indio de Gatún, *Goldman 2778* (US). Madden Forest Preserve, Las Cruces Trail and Highway, *Lewis et al. 5305* (MO). Quebrada San Antonio, 2.0–3.5 km N of Gamboa, *Nee 9466* (MO, USF). BARRO COLORADO ISLAND: *Aviles 28* (F); *Bailey 205* (F); *Brown 102a* (F); *Croat 5782, 8021, 12217, 12933, 14105A, 14554* (all MO); *Foster 654* (DUKE); *Hunnewell 16463* (GH); *Shattuck 566* (F, MO); *Standley 40916* (US); *Wetmore et al. 10* (GH), *10A* (F, GH); *Zetek 3845* (F). COCLÉ: El Valle de Antón, *Allen 1807* (F, GH, MO, US). Cerro Pilón, *Croat 22938* (F, MO, US). El Valle de Antón, *Dwyer 10529* (MO). Cerro Pilón, *Dwyer & Lallathin 8640* (MO). El Valle de Antón, *Lewis et al. 1778* (MO). Boca del Toabre at confluence of Río Toabre and Río Cocle del Norte, *Lewis et al. 5574* (MO). COLÓN: 1–3 mi W of Portobelo, *Gentry 1760* (F, MO). Ca. 0.5 km from Río Buenaventura near Portobelo, *Kennedy & Gra 2246* (F, MO, US). 10 mi SW of Portobelo and 2–4 mi from coast, *Liesner 1036* (MO). Río Lagarto region, Gatún Lake, *Seibert 1529* (US). DARIÉN: S slope of W peak of Cerro Tacarcuna Massif, *Gentry & Mori 13965, 13965A* (both MO). PANAMÁ: Hills above Campana, *Allen 1691* (MO). 5 mi above Panamerican Highway on road to Cerro Azul, *Croat 11521* (MO). Along trail between Río Maje and Quebrada Brava, *Croat 34636* (MO). Capira, NW side of Cerro Trinidad, *Foster 2094* (DUKE). Cerro Campana, *Gentry 4909* (MO). El Llano-Cartí Road, 9.6 km from Panamerican Highway, *Mori & Kallunki 1828* (MO). VERAGUAS: Río Segundo Brasso, 8 km beyond Escuela Agrícola Alto de Piedra beyond Santa Fé, *Croat 25562* (MO). Along road between Escuela Agrícola Alto de Piedra above Santa Fé and Río Dos Bocas, ca. 10 km from the Escuela, *Croat 25899* (MO). Valley of Río Dos Bocas between Escuela Agrícola and Calovébora, 15.6 km NW of Santa Fé, *Croat 27765* (MO). NW of Santa Fé, 8.8 km from Escuela Agrícola Alto de Piedra, *Mori et al. 4016* (MO, USF). NW of Santa Fé, 2 km Escuela Agrícola Alto de Piedra, lower slopes of Cerro Tuté, *Mori & Kallunki 5228* (MO, USF).

11. LAGENARIA

Lagenaria Ser., Mém. Soc. Phys. Genève 3(1): 25. 1825. TYPE: *L. vulgaris* Ser.

Annual, monoecious, tendriled *vines*; stems 5- to 10-sulcate. *Leaves* petiolate, simple; petiole biglandular at the apex; tendrils 2-branched. *Staminate flowers* solitary, long pedunculate; hypanthium narrow campanulate or funnelform; calyx 5-lobate; petals 5, white, free to the base; stamens 3, borne on the hypanthium wall, the filaments free, the anthers free or slightly connate, 1 unilocular, 2 bi-

locular, the theca flexuous; pistillodium glandiform. *Pistillate flowers* solitary, axillary; hypanthium tube cupuliform; corolla as in the staminate; ovary ovoid to cylindrical, 3-carpellate, the ovules numerous, horizontal, the style short, thick, the stigmas 3, bilobate thick; staminodia 3, minute. *Fruits* yellowish or whitish, variable in shape and size, usually large, indehiscent, the cortex woody, the flesh spongy; seeds white, obovate to triangular, compressed, marginate, the apex truncate or bidentate, rarely rounded.

This is a monotypic genus with two subspecies: *L. siceraria* (Molina) Standl. var. *siceraria* occurring in the Americas and Africa and *L. siceraria* subsp. *asiatica* (Kobiakova) Heiser occurring in Asia and the Pacific region. Only the former subspecies is found in Panama.

1. **Lagenaria siceraria** (Molina) Standley, Field Mus. Nat. Hist., Bot. Ser. 3: 435. 1930.—Fig. 11.

Cucurbita lagenaria L., Sp. Pl. 1010. 1753. TYPE: without locality (LINN 1151.1, microfiche).
C. leucantha Duch. in Lam., Encycl. Méth. Bot. 2: 150. 1786. TYPE: not known.
C. siceraria Molina, Saggio Storia Nat. Chili 133. 1782. TYPE: not known.
Lagenaria vulgaris Ser., Mém. Soc. Phys. Genève 3(1): 25. 1825. TYPE: not known.
L. lagenaria (L.) Cockerell, Bull. Torrey Bot. Club 19: 95. 1892
L. leucantha (Duch.) Rusby, Mem. Torrey Bot. Club 6: 43. 1896.
L. vulgaris subsp. *afrikana* Kobiakova, Trudy Prikl. Bot. 23: 1930. TYPE: not known.
L. siceraria var. *laevisperma* Millán, Darwiniana 7: 196. 1946. TYPE: Uruguay, *Rosengurtt* (SI, holotype, not seen).
L. bicornuta Chakr., Ann. Missouri Bot. Gard. 55: 69. 1968. TYPE: Ghana, *Chakravarty C1001* (K, not seen).

Monoecious, tendriled, high climbing *vines*; stems thick, angled, pubescent when young, soon glabrescent. *Leaves* cordate orbicular, 10–40 cm long, nearly or equally as wide, angulate or shallowly 3-lobate, the apex rounded to acute, the base cordate, the margin minutely dentate, chartaceous, the upper and the lower surfaces pubescent, especially on the veins, obscurely white pustulate above, biglandular at the base of the blade, the glands small, sessile, elliptic; petioles 6–10 cm long, striate, pubescent; tendrils 2-branched for ca. ⅔ their length, pubescent when young, soon glabrescent. *Staminate flowers* solitary; peduncles about as long as the petiole of the subtending leaf; calyx 2–3 cm long, tomentose, lobes 3–4 mm long, narrowly triangular; petals oblong ovate, spreading, emarginate and mucronate at the apex, 5-nerved, puberulent on both the surfaces; filaments free, glabrate, 3–4 mm long, the anthers 8–10 mm long, free or slightly connate, the theca flexuous; pistillode glanduliform. *Pistillate flowers* solitary, the peduncle subequalling the petiole of the subtending leaf; calyx tube 3–4 mm long, lobes 2–3 mm long, narrowly triangular, tomentose; corolla as in the staminate flowers; ovary ovoid to cylindrical, tomentose, the style short, thick, stigmas 3, bilobate, thick; staminodia 3, ca. 1 mm long. *Fruits* whitish or yellowish, variable in size and shape but generally large, indehiscent, cortex woody, flesh spongy; seeds white, obovate to triangular, 7–20 mm long, compressed, marginate, the apex truncate or bidentate, rarely rounded.

Lagenaria siceraria is believed to be native to tropical Africa. However, archeological fragments of this species found in the Americas date back to 7000–

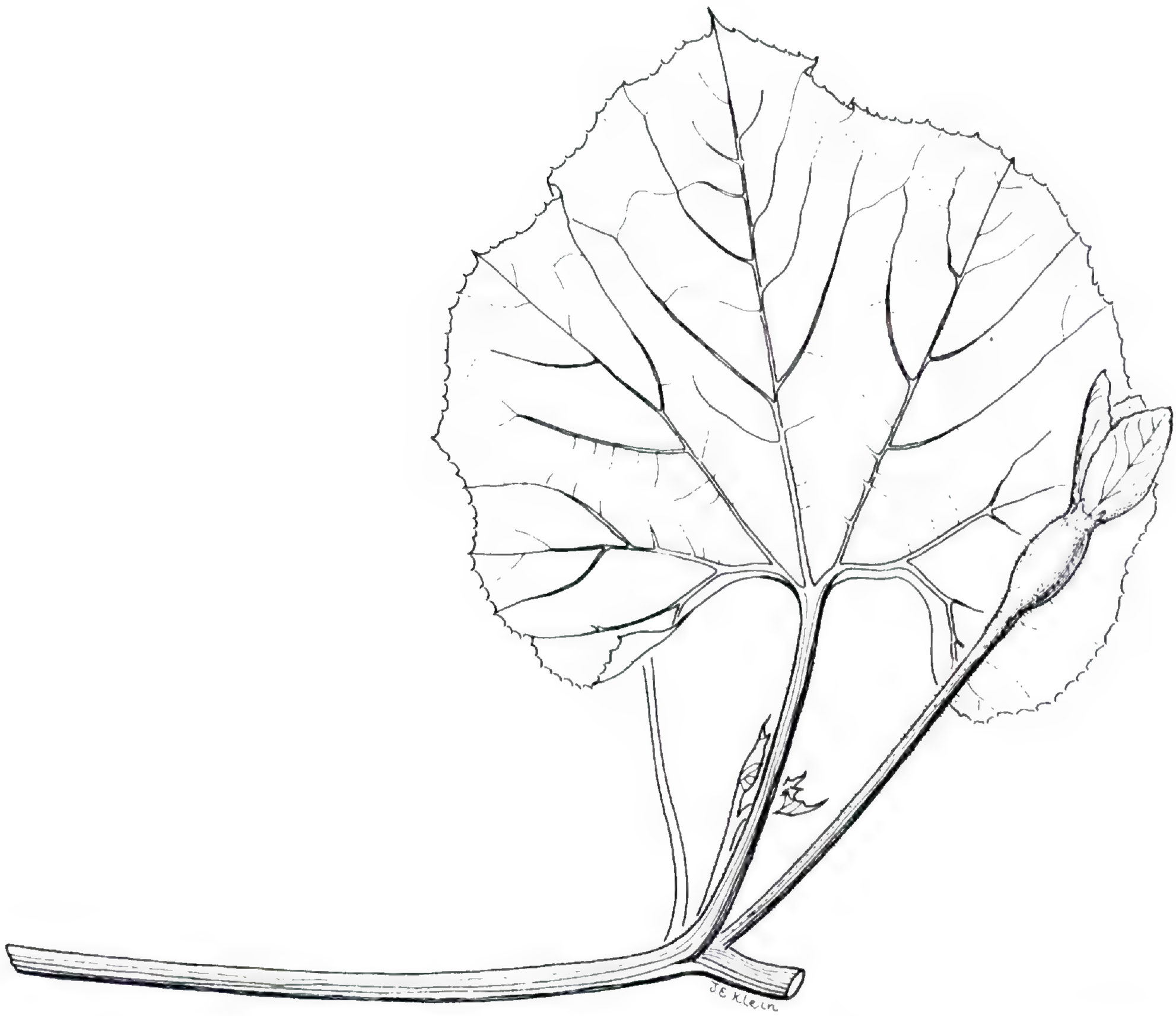


FIGURE 11. *Lagenaria siceraria* (Molina) Standl. Habit (×3/5). [After *Romero-Castañeda 11059*—Colombia].

5500 B.C. It has been suggested that the fruits floated from Africa to the New World and became established there. However, trans-Atlantic or trans-Pacific migration by primitive people cannot be entirely discounted regarding the spread of this species.

The species is extremely variable. Being in cultivation such a long time, numerous forms have been selected.

Lagenaria siceraria is commonly referred to as the "bottle gourd" in English speaking countries. In Panama it is referred to as "tule de mate" or "calabaza." In other Spanish speaking countries it is called "tarro," "tecomate," "tecomatillo," "tol," and "bule," in addition to "calabaza." It is widely used in both the Neo- and Paleotropics to make containers, ladles, musical instruments, and numerous other items of ornamental and everyday use.

Although the species is probably widely distributed in Panama, only the following collection was seen during this study.

COCLÉ: Olá, *Pittier 5028* (US). COLÓN: Viento Frio, *Pittier 4138* (US). PANAMÁ: Isla Espiritu Santo, *Duke 10445* (MO).

12. LUFFA

Luffa Miller, Gard. Dict., abr. ed. 4. 1754. TYPE: *L. aegyptiaca* Miller.

Trevouxia Scop., Introd. 152. 1777. TYPE: not designated.
Turia Forsk. ex J.F. Gmelin, Syst. Nat. 2: 303, 403. 1791. TYPE: not designated.
Poppya Neck. ex M.J. Roem., Fam. Nat. Syn. Monogr. 2: 59. 1846. TYPE: *P. operculata* (L.) M. Roem.

Monoecious, tendriled *vines*: stems 5- to 10-sulcate. *Leaves* petiolate, simple, 5- to 7-lobate, rarely subentire; tendrils simple or 2- to 5-branched. *Staminate flowers* in racemes, axillary; calyx campanulate or turbinate, 5-lobate; petals 5, free; stamens 3 (in ours), borne on the hypanthium tube, free, the anthers linear, flexuous, variously unilocular or bilocular; pistillodium glanduliform or absent. *Pistillate flowers* solitary in the axils of the same leaves as the staminate inflorescences; calyx and corolla similar to those of the staminate flowers; ovary elongate, 3-carpellate, the ovules numerous, horizontal, the styles 3, connate, the stigmas 3, bilobate; staminodia 3, rarely 4 or 5. *Fruits* cylindrical, fusiform, ellipsoidal, or clavate, smooth, tuberculate, echinate, or acutely ribbed, operulate at the apex, the style persistent, the interior filled with a coarse fibrous mass (vascular bundle net); seeds oblong, compressed, winged or wingless, the testa smooth or rugose.

The genus includes 6–10 species mostly native in the tropics and subtropics of the Old World. A single species is native to the New World. Some species are cultivated and widely distributed. One native and one introduced species occurs in Panama.

a. Fruit ellipsoidal, 5–10 cm long, tuberculate or shortly echinate; petals 1.0–1.5 cm long ..... 2. *L. operculata*
aa. Fruit cylindrical or fusiform, (10–) 15–30 cm long, smooth; petals 2–3 cm long ..... 1. *L. aegyptiaca*

1. **Luffa aegyptiaca**[10] Miller, Gard. Dict. abr. ed. 8. 1768, based on *Momordica luffa* L., 1753.—FIG. 12.

Momordica cylindrica L., Sp. Pl. 1009. 1753. TYPE: without locality, Herb. Linn. 1150.9 (LINN, not seen; microfiche MO).
Momordica luffa L., Sp. Pl. 1009. 1753. TYPE: India, Herb. Linn. 1150.6 (LINN, not seen; microfiche MO).

Monoecious, tendriled *vines*; stems 5- to 10-sulcate, pubescent to glabrate. *Leaves* with the blades suborbicular in outline, 10–25 cm long, as wide or slightly wider than long, apex acuminate to caudate, the base deeply cordate, the margin denticulate, chartaceous, the upper and the lower surfaces scabrous with pustular based trichomes; petioles 4–12 cm long, slender, pubescent to glabrate, striate; tendrils 3- to 5-branched, pubescent to glabrate. *Staminate flowers* in axillary racemes, the rachis 10–35 cm long, appressed pubescent, glabrate toward the base, 10- to 30-flowered in the upper half, the pedicels 1–2 cm long, pubescent; calyx campanulate, lobed for ¾ or more its length, the lobes 10–15 mm

[10] For additional synonymy, see Cogniaux and Harms (1924) under *Luffa cylindrica* (L.) Roem. Also see Schubert (Taxon 24: 171–177. 1975) for discussion of use of *L. aegyptiaca* over *L. cylindrica*.

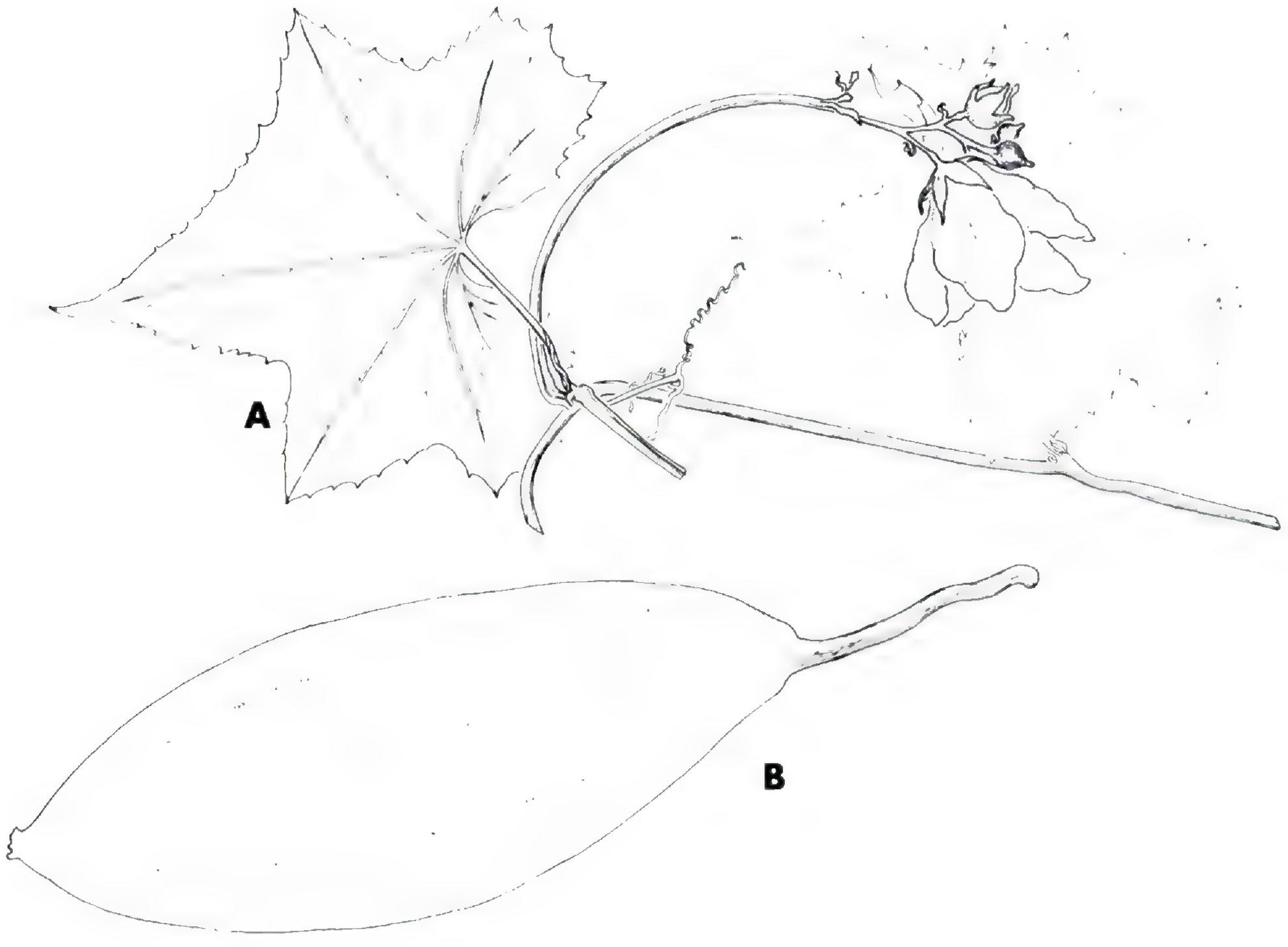


FIGURE 12. *Luffa aegyptiaca* Mill.—A. Habit (×½). [After *Croat 14498*].—B. Fruit (×½). [After *D'Arcy & Croat 4189*].

long, lanceolate, acuminate, appressed pubescent; petals yellow, oblong cuneate to obovate, 2–3(–4) cm long, mucronate, the outer surface puberulent, especially toward the base and on the nerves, the inner surface stipitate glandular, also with a few scattered nonglandular hairs, prominently ribbed, the stamens 3, free, the filaments 6–10 mm long, slender, puberulent, ciliate at the base, the anthers flexuous. *Pistillate flowers* solitary, axillary; peduncles 2–10 cm long; calyx and corolla as in the staminate flowers; ovary fusiform, ca. 1.5 cm long, appressed pubescent, 3-carpellate, the ovules numerous, horizontal, the styles connate, the stigmas 3, bilobate, densely papillate, staminodia 5, ca. 1 mm long, pubescent, the tip glabrous. *Fruits* green, longitudinally striate with darker markings, cylindrical or fusiform, 10–30 cm long, ecostate, dehiscent by a conical, long-beaked operculum; seeds gray, mottled with darker markings, ovoid, compressed, 8–12 mm long, 7–10 mm wide, the margin narrowly winged, 2 oblique bumps present above the hilum on each surface, the testa granulate.

Luffa aegyptiaca, native to the Old World tropics, is spontaneous after cultivation and naturalized in Panama as well as other parts of the New World tropics. It usually is found along roadsides, in thickets, and near habitations at low elevations. The species is known in Panama and other parts of the Neotropics as "calabazo," "esponga," "sponge cucumber," "vegetable sponge," or "spongegourd." It is used locally as a substitute for sponge or cooked and eaten as a vegetable.

CANAL ZONE: Balboa, *Celestine 4* (US). Gatún, *Hayes 146* (NY). Government forest along Las Cruces Trail, *Hunter & Allen 684* (MO). Río Grande, near Culebra, *Pittier 2115* (NY, US). Balboa, *Standley 25542* (US). CHIRIQUÍ: San Bartolo Arriba W of Puerto Armuelles, *Croat 26695* (MO). Between Río Tinta and Río Tabasara along main highway, *Woodson et al. 417* (MO). COCLÉ: El Cope, road to Panamerican Highway, ca. 3 mi from El Cope, *McDaniel & Cooke 14773* (FSU). Between Aguadulce and Antón, *Woodson et al. 1214* (GH, MO). DARIÉN: Río Sabana, ca. 4 mi above Santa Fé, *Duke 10225* (MO). Río Balsa, above Tucutí, *Terry & Terry 1407* (F, GH, MO). HERRERA: 10 mi S of Ocú, *Tyson et al. 2819* (MO). LOS SANTOS: 3 mi S of Carreta, ca. 5 mi S of Las Tables, *Burch 1232* (GH, MO, US). 3 mi S of Chitré, *D'Arcy & Croat 4189* (GH, MO, NY). PANAMÁ: El Llano, *Croat 14498* (MO). Around town of Pacora, *D'Arcy 9638* (MO). 6 mi E of Chepo on Panamerican Highway, *Duke 4089* (GH, MO, US). El Llano, *Duke 5842* (GH, MO). Isla de Pedro Gonzales, *Dwyer 1692* (F, MO). Next to National Brewery near Transisthmian Highway, Tocumen, *Dwyer 4095* (MO). Vera Cruz, *Lewis et al. 2994* (MO). Next to National Brewery near Transisthmian Highway, *Taylor* (MO). SAN BLAS: Through cultivation on mainland in front of Ustupo, *D'Arcy 9539* (MO). VERAGUAS: W of Soná, *Allen 1062* (F, GH, MO). Santiago, 4 mi from Transisthmian Highway toward Atalaya, *Dwyer & Kirkbride 7415* (MO). Ponuga, *Dwyer & Kirkbride 7446* (GH, MO). Cañazas, *Tyson 3606* (MO).

2. **Luffa operculata** (L.) Cogn. in Mart., Fl. Bras. 6(4): 12. 1878.

Momordica operculata L., Syst. Nat. ed. 10. 1433. 1759. SYNTYPES: without locality Herb. Linn. 1150.4 & 1150.5 (LINN, neither seen; microfiches MO).
Cucumis sepium G.F.W. Meyer, Prim. Fl. Esseq. 276. 1818. TYPE: not known.
Momordica purgans Mart. in Spix & Mart., Reise Brasil. 2: 546. 1828. TYPE: not known.
Elaterium quinquefidum Hook. & Arn., Bot. Beech. Voy. 292. 1841. TYPE: not known.
Momordica quinquefida (Hook. & Arn.) Hook. & Arn., Bot. Beech. Voy. 424. 1841.
Luffa purgens (Mart.) Mart., Syst. Mat. Med. Veg. Brasil. 81. 1843.
Poppya operculata (L.) M.J. Roem., Fam. Nat. Syn. Monogr. 2: 59. 1846.
Luffa quinquefida (Hook. & Arn.) Seem., Bot. Voy. Herald 285. 1853.
L. operculata var. *lobata* Cogn. in Mart., Fl. Bras. 6(4): 13. 1878.
L. operculata var. *intermedia* Cogn., Contr. U.S. Natl. Herb. 1: 330. 1895. TYPE: Mexico, *Palmer 770* (US, holotype, not seen).
L. astorii Svens., Amer. J. Bot. 22: 256. 1935. TYPE: Ecuador, *Svenson 159* (NY, holotype, not seen).

Monoecious, tendriled *vines*; stems 5- to 10-sulcate, hispidulous, puberulent, or glabrate. *Leaves* suborbicular, 5–15 cm long, as wide or slightly wider than long, shallowly to deeply 5- to 7-lobate, sometimes subentire, the apex rounded to acute, the base deeply cordate, the margin dentate, somewhat undulate, chartaceous, the upper surface scabrous with pustular-based trichomes, the lower surface scabrous; petioles 3–8 cm long, slender, hispid or pubescent, striate; tendrils 2- to 3-branched, hispid or pubescent. *Staminate flowers* in axillary racemes, the rachis 5–15 cm long, appressed puberulent; calyx campanulate, 5-lobate to ⅔ its length, the lobes 5–8 mm long, lanceolate, acuminate, appressed pubescent; petals yellow, obovate, 8–15 mm long, mucronate, glabrate; stamens 3, free, the filaments 2–3 mm long, slender ciliate at the base, the anthers flexuous. *Pistillate flowers* solitary, axillary; peduncles 1–2 cm long; calyx and corolla as in the staminate flowers; ovary fusiform, ca. 1 cm long, appressed pubescent, tuberculate, 3-carpellate, the ovules numerous, horizontal, the styles connate, the stigmas 3, bilobate, irregularly curved and coralloid, densely papillate, the staminodia 5, ca. 1 mm long, puberulent. *Fruits* green or gray green, ellipsoidal, 5–10 cm long, 8- to 10-costate, costae tuberculate or shortly echinate, puberulent, glabrate in age, dehiscent by a conical, long-beaked operculum; seeds gray or brown, faintly mottled with darker markings, ovoid, compressed, 6–10 mm long,

4–5 mm wide, 2 oblique bumps present above the hilum on each face, the testa smooth or rugulose.

The somewhat variable *Luffa operculata* is the only species native to the American tropics and subtropics. It ranges from northern Mexico south to Peru and Ecuador. It grows at low elevations, scrambling over rocks and low shrubs in thickets, open areas, usually near the edge of rivers, ponds, or in coastal plains. It is known in Panama from a single collection, but was also reported from Matías Hernández by Standley (1928). It probably is more common than collections indicate.

The species is known in Panama as "espongillo" or "spongegourd." It is used locally in Central and South America medicinally and as a substitute for a sponge.

CANAL ZONE: Fort Sherman, beach and lighthouse, *Burch et al. 1009* (GH, MO, US). PANAMÁ: Agricultural experiment station at Matias Hernández, *Pittier 6936* (US).

13. MELOTHRIA

Melothria L., Sp. Pl. 1753; Gen. Pl., ed. 5. 21. 1754. TYPE: *M. pendula* L.

Landersia Macf., Fl. Jam. 2: 142. 1837. TYPE: not designated.
Aechmandra Arn., J. Bot. (Hooker) 3: 274. 1841. TYPE: not designated.
Diclidostigma Kunze, Linnaea 17: 576. 1843. TYPE: *D. melothrioides* Kunze.

Monoecious, tendriled *vines*; stems 5- to 10-sulcate. *Leaves* petiolate, simple, entire or lobate; tendrils simple. *Staminate flowers* axillary, racemose; calyx campanulate to subcylindric, 5-lobate; corolla yellow or white, deeply 5-lobate; stamens 3, free, inserted on the hypanthium wall, the anthers oblong or suborbicular, 1 unilocular, 2 bilocular; pistillode globose or conic. *Pistillate flowers* solitary; calyx and corolla as in the staminate flowers; ovary ovoid to fusiform, 3-carpellate, the ovules numerous, horizontal, the styles 3, connate, short, the base surrounded by a ringlike disc, the stigmas 3, linear; staminodia 3. *Fruit* ovoid to fusiform; seeds ovoid or ellipsoidal, compressed, sericeous.

Melothria is a genus of about 10 species confined primarily to the New World tropics. Cogniaux placed 85 species in the genus. A narrower view is taken here following Jeffrey (1962), recognizing the Old World genera *Zehneria*, *Solena*, and *Mukia* as distinct from *Melothria*.

a. Leaves 5- to 7-lobate nearly to base ..... 4. *M. trilobata*
aa. Leaves cordate to sagittate, rarely shallowly 3- to 5-lobate.
  b. Fruit 0.7–1.5 cm long, solid green or black at maturity ..... 2. *M. pendula*
  bb. Fruit 2.5–7.0 cm long, not solid green or black at maturity.
    c. Fruit irregularly light and dark green striped at maturity, pulp greenish white, exocarp thin; corolla yellow ..... 3. *M. scabra*
    cc. Fruit yellow or orange at maturity, pulp orange, exocarp subligneous; corolla white ..... 1. *M. dulcis*

1. **Melothria dulcis** Wunderlin, Phytologia 38: 220. 1978. TYPE: Panama, *Croat 16693* (MO, holotype; MO, isotype).

Vines; stems minutely scabrous, glabrate in age. *Leaves* cordate, 8–14 cm long, 6–10 cm wide, the apex acuminate, the base deeply cordate, the margin

undulate, remotely denticulate, chartaceous, the upper surface minutely white pustulate, slightly scabrous to glabrate, sparsely short strigose on the nerves, the lower surface glabrate; petioles 3–7 cm long, glabrate; tendrils simple, glabrate. *Staminate flowers* axillary, racemose; peduncles ca. 2 cm long; calyx tube narrowly campanulate, ca. 5 mm long, glabrous, 10-nerved, the lobes triangular lanceolate, ca. 1 mm long; corolla white, lobes oblong, 3.0–3.5 mm long, the apex emarginate, pubescent on both the surfaces, reflexed; anthers oblong, ca. 2.5–3.0 mm long, papillose at the apex, ciliate; pistillode conical, glabrous. *Pistillate flowers* solitary in the same axils as the staminate flowers; peduncle 2–3 cm long; other details unknown. *Fruits* yellow to orange, ellipsoidal to subspherical, 5–7 cm long, 4.5–6 cm in diameter, smooth, glabrous, exocarp subligneous, mesocarp orange, sweet; seeds white sericeous, narrowly ovate, 9–10 mm long, 5–6 mm wide.

Melothria dulcis occurs in wet forests and along streams at 350–400 m elevation. It is endemic to Panama and is known only from Panama, Darién, and Colón provinces and the Canal Zone. It is easily distinguished from the other *Melothria* species in Panama by its large orange fruit and white corolla. The mesocarp is said to be sweet and edible.

CANAL ZONE: Pipeline Road, *Croat 16693* (MO). COLÓN: Río Guanche, *Foster 2812* (MO). DARIÉN: Río Balsa, between Río Areti and Río Manane, *Duke 8761* (MO). PANAMÁ: El Llano-Cartí Road, 7–12 km from Panamerican Highway, *Croat 25165* (MO). El Llano-Cartí Road, 10–12 km from junction with Panamerican Highway, *Mori & Kallunki 2861* (MO, USF). El Llano-Cartí Road, 8.5 km from Panamerican Highway, *Mori et al. 4551* (MO, USF).

2. **Melothria pendula**[11] L., Sp. Pl. 35. 1753. TYPE: without locality and collector (LINN 51.1, microfiche).

Bryonia guadalupensis Spreng., Syst. Veg. 3: 580. 1881. TYPE: not known.
Melothria fluminensis Gardner, Hook. Lond. J. Bot. 1: 173. 1842. TYPE: Brazil, *Gardner 45* (US, isotype; MO, photo of isotype at G).
M. guadalupensis (Spreng.) Cogn. in DC., Monogr. Phan. 3: 580. 1881.

Vines; stems scabrous to glabrate. *Leaves* with blades cordate to sagittate, rarely shallowly 3- to 5-lobate (in other parts of the range sometimes deeply 3- to 5-lobate), 3–7(–10) cm long, to as wide as long, the apex acuminate to caudate, the base cordate, the margin undulate, minutely and remotely toothed, chartaceous, the upper and the lower surfaces scabrous with white pustular based trichomes; petioles 1–4 cm long, scabrous to glabrate; tendrils simple, glabrate. *Staminate flowers* in axillary, long pedunculate racemes, the rachis 2–3 cm long, filiform, glabrate, 2- to 6-flowered; pedicels 2–3 mm long; calyx campanulate, the lobes subulate, ca. 0.5 mm long, sparsely pilose; corolla yellow, the lobes ovate oblong, acute, spreading, papillose puberulent on the inner surface, puberulent on the outer surface; anthers narrowly oblong, ciliate on the margin; pistillode globose. *Pistillate flowers* solitary; peduncles 1–3 cm long, glabrate; calyx and corolla as in the staminate flowers; ovary ellipsoidal, glabrous, smooth. *Fruits*

[11] See Cogniaux (1916) for complete synonymy under *M. pendula*, *M. guadalupensis*, and *M. fluminensis*. Also, most of the infraspecific taxa recognized by Cogniaux under these three species should probably be referred here.

black, ovoid to elliptical, 0.7–1.5(–2.0) cm long, 0.7–1.0 cm in diameter, smooth, glabrous, baccate; seeds white sericeous, ovoid, 4–5 mm long, 2–3 mm wide.

Melothria pendula is a widespread weedy species occurring in disturbed sites and thickets from southern United States south through the Caribbean and Central America to Argentina. It is common in Panama.

This species is here interpreted as a highly variable and polymorphic species perhaps consisting of several infraspecific taxa or at least biotypes. No characters could be found to consistently differentiate between more northern, widespread *M. pendula* and the more southerly *M. fluminensis* and *M. guadalupensis*.

BOCAS DEL TORO: Nievecita, *Bartlett 1* (MO). Santa Catalina, *Blackwell et al. 2756* (MO). Region of Almirante, *Cooper 184* (F). Water Valley, Chiriquí Lagoon, *Wedel 819* (GH, MO), *1037* (GH, MO, US), *1496* (GH, MO), *1796* (MO). Nievecita, *Woodson et al. 1869* (F, MO, NY). CANAL ZONE: Juan Mina, *Bartlett & Lasser 16754* (MICH). 3 millas N del muelle del Laboratorio de Entomologia, Division de Sanidad, Río Chagres, Gamboa, *Correa & Lazor 1572* (MO). Summit Hills Golf Course, *Croat 12245* (MO). Coastal Island beyond Fort Amador, *D'Arcy 9226* (MO). Fort Kobbe, *Duke 3946* (MO). Corrosion Laboratory, Miraflores Locks, *Duke 4440A* (MO). Beach at Fort Kobbe, *Duke 4709* (GH, MO, US). Albrook, *Dwyer 6635* (MO). Chagres, *Fendler 123* (GH, MO, US). C-29 beyond Summit, *Harvey 5213* (F). Garden of Gatún Station, *Hayes 57* (NY). Fort Kobbe, *Kenoyer 569* (US). Ancón Hill, *Killip 3038* (US). Between Frijoles and Monte Lirio, *Killip 12167* (US). 1 mi N of Gamboa on Chagres River, *Lazor & Boreham 2935* (FSU, MO). Margarita Swamp S of France Field, *Maxon & Valentine 7057* (US). Ancón, *Piper 6026* (US). W slope of Ancón Hill, *Seibert 387* (GH, MO, NY). Sosa Hill, Balboa, *Standley 25283* (US). Balboa, *Standley 25544, 25626, 27138* (all US). Hills W of the canal, near Gatún, *Standley 27238* (US). Gamboa, *Standley 28361* (US). Near Fort Randolf, *Standley 28724* (US). Río Pedro Miguel, near East Paraiso, *Standley 29924* (US). Balboa, *Standley 30897* (US). Fort Sherman, *Standley 20994* (US). Corrosion Laboratory, Miraflores Locks, *Stern et al. 67* (GH, MO, US). Miraflores Locks, *Tyson 1150, 1596* (both FSU, MO). Gamboa at horse stables, *Tyson & Lazor 6322* (FSU). BARRO COLORADO ISLAND: *Aviles 65A* (MO); *Bailey & Bailey 128* (F); *Croat 4078, 4149, 4166, 5250, 5638, 5893, 6361, 6372A, 6400, 7020, 8277, 11944* (all MO); *Ebinger 643* (F, MO); *Foster 1440* (DUKE); *Shattuck 536* (F, MO); *Starry 196* (F, MO), *279* (F); *Woodworth & Vestal 547* (F, GH, MO). CHIRIQUÍ: Valley of Upper Río Chiriquí Viejo, Monte Lirio, *Seibert 394* (GH, MO, NY). COCLÉ: Bismark above Penonomé, *Williams 283* (NY). Penonomé and vicinity, *Williams 325* (NY). COLÓN: Along Río Guanche, ca. 3–5 mi inland, *Croat 26153* (MO). Garotte, ca. 10 km NE of Portobelo, *D'Arcy 3995* (MO). DARIÉN: El Real, *Allen 949* (F, GH, MO, US). Road to Pinogana near El Real, *Croat & Porter 15481* (MO). Río Pirre, *Duke 4959* (GH, MO); *Kennedy 2876* (MO). Mannene, *Kirkbride & Bristan 1573* (MO). Without other locality, *Macbride 2704* (F). Río Balsa, above Tucutí, *Terry & Terry 1409* (F, GH, MO). HERRERA: Divisa, *Dwyer 2464* (MO, USF). LOS SANTOS: Between Tonosí and Macaracas, *Oliver et al. 3541* (MO). Los Asientos, *Wendehake 43* (MO). PANAMÁ: Las Cumbres, *Aguilar 30* (MO). Between Río Bayano Dam and Cañitas, *D'Arcy 9386* (MO). Camino de Las Sabanas, *Heriberto 193* (NY, US). San José Island, *Johnston 397* (GH). Taboga Island, *Macbride 2753* (F). Sabanas, N of Panama City, *Paul 575* (US). Taboga Island, Gulf of Panama, *Pittier 3558* (US); *Standley 27070* (US). Río Tocumen, *Standley 29462* (US). Between Las Sabanas and Matias Hernandez, *Standley 31845* (US). 2 mi S of Tocumen Airport, *Tyson & Clewell 5891* (FSU). SAN BLAS: Puerto Obaldía, *Croat 17006* (MO). Hydro Camp Cuadí on Río Cuadí, *Duke 15469* (USF). Puerto Obaldía, *Gentry 1560* (MO). Mainland opposite Achituppu, *Lewis et al. 134* (GH, MO). Puerto Obaldía, *Pittier 4376* (US).

3. **Melothria scabra** Naud., Ann. Sci. Nat. Bot., sér. 5. 6: 10. 1867. TYPE: not known.

M. donnell-smithii Cogn., Bot. Gaz. (Crawfordsville) 16: 9. 1891. TYPE: Guatemala, *Smith 2203* (US, holotype).

M. donnell-smithii var. *hirtella* Cogn., Bot. Gaz. (Crawfordsville) 16: 9. 1891. TYPE: *Smith 2206* (US, holotype).

M. donnell-smithii var. *rotundifolia* Cogn., Bot. Gaz. (Crawfordsville) 16: 9. 1891. TYPE: Guatemala, *Smith 2208* (US, holotype).
M. pendula Mottet, Rev. Hort. 660. 1900; non L., 1753. TYPE: not known.

Vines; stems scabrous, short pilose, or glabrate. *Leaves* cordate, entire, or shallowly 3- to 5-lobate, 3–7(–10) cm long, up to as wide as long, the apex acuminate to caudate, the base cordate, the margin undulate or dentate, minutely and remotely toothed, chartaceous, the upper surface scabrous with white pustulate based trichomes, short pilose on the veins, the lower surface short pilose, at least on the veins; petioles 2–4 cm long, short pilose, scabrous, or glabrate; tendrils simple, glabrate. *Staminate flowers* in axillary, long pedunculate racemes, the rachis 2–4 cm long, filiform, short pilose or glabrate, 2- to 7-flowered; pedicels 2–3 mm long; calyx campanulate, the lobes triangular, ca. 1 mm long, short pilose or glabrate; corolla yellow, the lobes ovate oblong, rounded to slightly emarginate, spreading, the outer surface appressed pubescent, the inner surface glabrate; anthers subquadrate, ciliate; pistillode globose, glabrous. *Pistillate flowers* solitary; peduncles 1–3 cm long, glabrate; calyx and corolla as in the staminate flowers; ovary ellipsoid, glabrate, smooth; staminodia minute, antheriferous. *Fruits* green with darker green stripes, 2.5–4.0 cm long, 1.5–2.5 cm in diameter, smooth, glabrous, baccate; seeds white sericeous, ovoid, 2–4 mm long, 2.0–2.5 mm wide.

Melothria scabra occurs in moist forests and thickets from Mexico south to Panama. It is easily confused with the more common *M. pendula*, but differs in its larger, dark and light green striped fruits. Sterile specimens of the two species often can not be distinguished with certainty.

BOCAS DEL TORO: Changuinola, *Carleton 75* (US). Chiriquicito to 5 mi S of Río Guarumo, *Lewis et al. 2090* (GH, MO). CANAL ZONE: Las Cascadas Plantation near summit, *Standley 25680, 25749* (both US). Cerro Gordo near Culebra, *Standley 25984, 26007* (both US). Old Las Cruces Trail between Fort Clayton and Corozal, *Standley 29118* (US). Las Cascadas Plantation near Summit, *Standley 29492* (US). CHIRIQUÍ: From Boquete to 3 mi N, *Lewis et al. 370* (GH, MO, US). COCLÉ: El Valle de Antón, *Lewis et al. 2587* (MO). PANAMÁ: 2 mi N of Río Chagres along Boyd Roosevelt Highway, *Blum & Tyson 1982* (FSU, MO). San José Island, *Johnston 397* (MO, US). Chimán, *Lewis et al. 3297* (MO). Around Alhajuela, *Pittier 2359* (US).

4. **Melothria trilobata** Cogn. in Mart., Fl. Bras. 6(4): 26. 1878. TYPE: Brazil, *Ule 8343* (MO, photo of isotype at B, specimen now destroyed).—FIG. 13.

M. trilobata var. *sphaerocarpa* Cogn. in DC., Monogr. Phan. 3: 578. 1881. TYPE: Colombia, *Andre 2477* (BR, holotype, not seen).
M. angustiloba Cogn. in DC., Monogr. Phan. 3: 579. 1881. TYPE: Mexico, *Hahn 106* (P, holotype, not seen).
M. trilobata var. *costaricensis* Cogn., Pflanzenr. 88 (IV, Fam. 275. II): 81. 1916. TYPE: Costa Rica, *Pittier 8504* (BR, holotype, not seen; US, isotype).
M. heterophylla Pittier, Bol. Soc. Venez. Ci. Nat. 6: 200. 1940. TYPE: Venezuela, *Pittier 9117* (US, holotype).

Vines; stems glabrate to sparsely crisped pilose. *Leaves* suborbicular in outline, 6–10 cm long, about as wide as long, deeply 5- to 7-lobate, the lobes acute to acuminate, apiculate at the apex, the base cordate, the margin undulate, remotely toothed, submembranaceous to chartaceous, the upper surface pubescent on the veins, minutely white pustulate, sometimes obscurely so, the lower

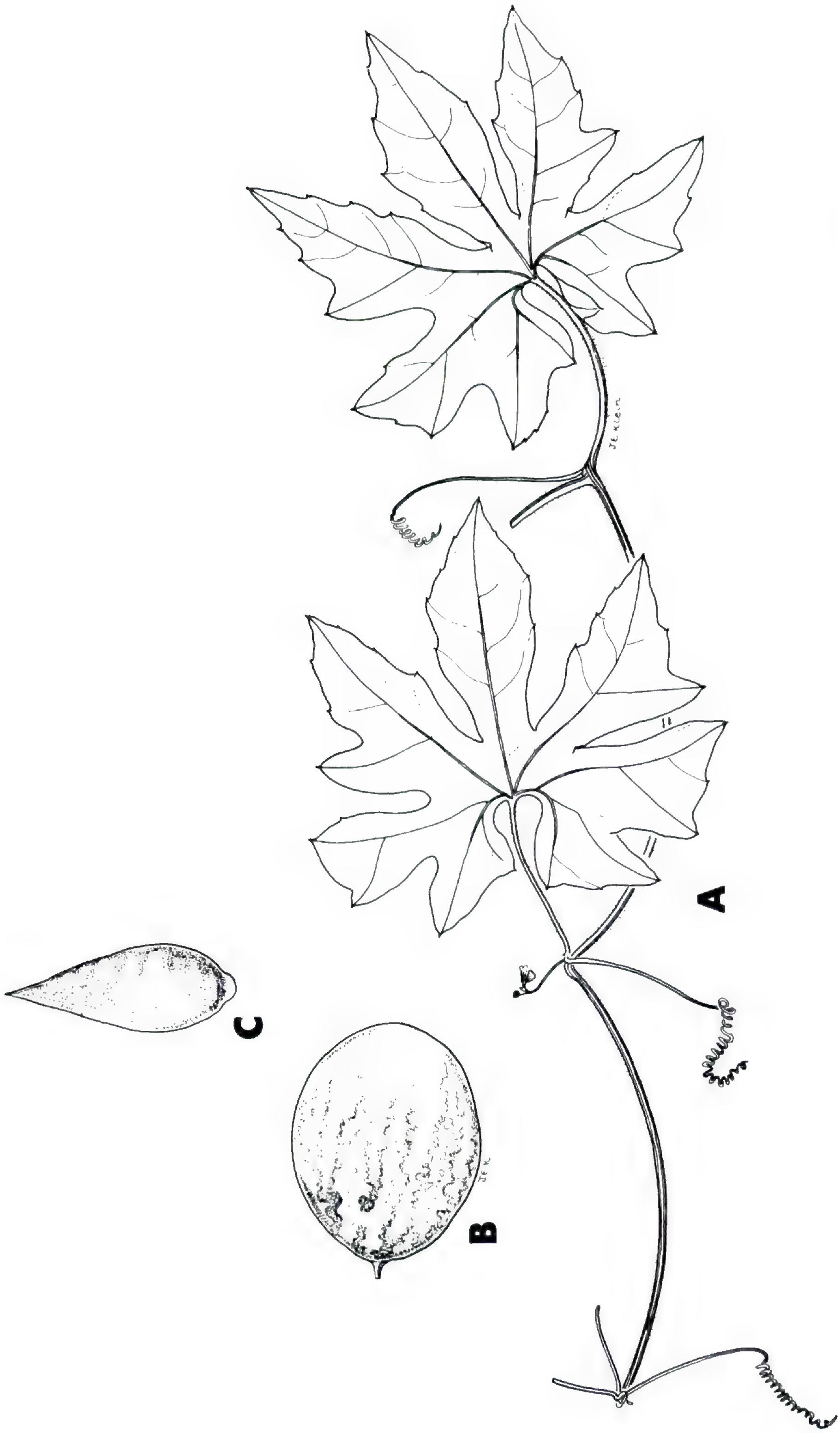


FIGURE 13. *Melothria trilobata* Cogn.—A. Habit (×⅔). [After *Wedel* 1532].—B. Fruit (×⅔). [After *Elias & Kirkbride* 1622].—C. Seed (×2). [After *Croat & Porter* 15537].

surface sparsely to densely pubescent; petioles 1–5 cm long, sparsely pilose and sometimes with short glandular trichomes; tendrils simple, sparsely pilose. *Staminate flowers* in axillary, long-pedunculate racemes, the rachis 1–3 cm long, filiform, sparsely pilose, 5- to 7-flowered; pedicels 4–6 mm long; calyx narrowly campanulate to subcylindric, the lobes 0.5–1.0 mm long, triangular, densely appressed pubescent at the apex, sparsely pubescent to glabrate towards the base; corolla yellow, the lobes ovate oblong, erect, the outer surface villous, the inner surface glabrate; anthers oblong, densely ciliate. *Pistillate flowers* solitary, in the same axils as the staminate flowers; peduncles stout, 5–8 mm long, sparsely pilose; calyx and corolla as in the staminate flowers; ovary ovoid, glabrous, smooth; staminodia minute. *Fruits* green with darker green stripes, ovoid, 4–5 cm long, 2.5–3.0 cm in diameter, smooth, glabrous, subbaccate; seeds white sericeous, narrowly ovoid, 5–7 mm long, 3–4 mm wide.

Melothria trilobata occurs in tropical moist forests and thickets from Mexico south to Colombia and Surinam. The species is somewhat variable vegetatively. It is locally known as "sandillita" in Panama. It is also used medicinally to some extent.

BOCAS DEL TORO: Nievecita, *Bartlett 3* (MO). Changuinola Valley, *Dunlap 397* (F, US). Water Valley, Chiriquí Lagoon, *Wedel 1532* (GH, MO), *1830* (GH, MO, US). CANAL ZONE: Summit Garden, *Croat 12829* (MO). Gaillard Highway, 2 mi NE of Summit Garden, *Croat 13796* (MO). Gaillard Highway, 1 mi NW of Summit Garden, *Croat 13918* (MO). Pipeline Road, ca. 5 mi N of Gamboa gate, *D'Arcy & D'Arcy 6106* (MO, US). Ancón Hill, *Duke 4594* (MO). Road C-21, *Duke 5769* (GH, MO). Coco Solo, near Army Corps of Engineers and U.S. Army Tropical Test Center, *Elias & Kirkbride 1622* (MO). Hills E of Curundu, *Harvey 5209* (F). ½ km W of Summit Gardens, *Nee 9491* (MO, USF). Ancón Hill, *Piper 5561* (US). Between Corozal and Ancón, *Pittier 2640* (US). Cerro Gordo, near Culebra, *Standley 25983* (US). Corozal, *Standley 27338* (US). Near Fort Randolf, *Standley 28703* (US). Along the old Las Cruces Trail, between Fort Clayton and Corozal, *Standley 29112* (US). Frances Field, *Stevens 183* (US). Culebra, *Stevens 949* (US). 2 mi N of Coclé, *Tyson 1634* (MO, SCZ). Miraflores Lake, *White 151* (MO). Barro Colorado Island, *Zetek 4996* (F, MO), *5591* (USF). COLÓN: San Miguel de la Borda, *Croat 9879* (MO). Between Frances Field Canal Zone and Cativa1, *Standley 30157* (US). DARIÉN: Río Pirre, *Croat & Porter 15537* (MO). Santa Fé, Río Sabana, *Duke 4139* (MO). LOS SANTOS: Los Toretos, *Dwyer 2442* (MO). PANAMÁ: Río Pacora, E of Panama City on Panama National Highway, *Bartlett & Lasser 16953* (MICH). Río Potrero, 2 mi from Arraijan, *Duke 4676* (GH, MO, US). San José Island, *Erlanson 504* (GH, NY, US). Chagres, Isthmus of Panama, *Fendler 124* (GH, US). San José Island, *Johnston 370* (US). Bald Hill Road, San José Island, *Johnston 371* (GH, MO). Las Sabanas, *Standley 25925* (US). Tumba Muerto Road near Panama, *Standley 29830* (US). Juan Diaz, *Standley 30628* (US). W of Chepo Road to Panama City, *Tyson 5372* (SCZ). SAN BLAS: Trail between Río Dian and Río Ailigandí, *Warner 223* (F).

14. MOMORDICA

Momordica L., Sp. Pl. 1009. 1753; Gen. Pl. ed. 5. 440. 1754. TYPE: *M. balsamina* L.

Amordica Neck., Elem. Bot. 1: 241. 1790. TYPE: not designated.
Muricia Loureio, Fl. Cochinch. 2: 596. 1790. TYPE: *M. cochinchinensis* Lour.
Zucca Comers. ex Juss., Gen. Pl. 398. 1798. TYPE: *Z. commersoniana* Ser.
Nevrosperma Raf., Am. Monthly Mag. 4: 40. 1818. TYPE: *N. cuspidata* Raf.

Monoecious or rarely dioecious, tendriled, scandent or prostrate *vines*; stems 5-sulcate. *Leaves* petiolate, simple or 3- to 9-foliolate; tendrils simple or 2-

branched. *Staminate flowers* in corymbs, racemes, or solitary, axillary; calyx campanulate, cupulate, or funnel-shaped, 5-lobate; corolla 5-lobate, rotate, or campanulate; stamens 3, rarely 2, the filaments free, the anthers connate, the thecas flexuous, forming an irregular head, ultimately free, 1 theca unilocular, 2 thecas bilocular. *Pistillate flowers* solitary, axillary; calyx and corolla as in the staminate flowers, ovary oblong or fusiform, 3-carpellate, each carpel few to many ovulate, ovules horizontal, the styles 3, connate, the stigmas 3, each bilobate. *Fruit* oblong, fusiform, or cylindrical, indehiscent or 3-valvate, often tuberculate or echinate; seeds turgid or compressed, the testa smooth, rugose, or rarely sculptured.

Momordica is a genus of about 60 species native to the Old World tropics and subtropics. Two species, *M. balsamina* and *M. charantia* are adventive in the New World tropics and subtropics. The latter species is found in Panama.

1. **Momordica charantia**[12] L., Sp. Pl. 1009. 1753. TYPE: ex China, in Hort. Upsaliensis, Herb. Linn. 1150: 2 (LINN, not seen; microfiche MO).—FIG. 14.

Leaves simple, reniform to suborbicular, 5- to 7-lobate to the middle or beyond, 3–6(–12) cm long and wide, the lobes oblong to spatulate, the apex obtuse and mucronate, the base cordate, the margin with obtuse to subacute teeth, submembranaceous to chartaceous, the upper surface minutely glandular, puberulent, at least on the veins; petiole 1–6 cm long, slender, striate; tendrils simple. *Staminate flowers* solitary, axillary; peduncle slender, 4–15 cm long, pubescent to puberulent, 5-lobate to near the middle, the lobes ovate lanceolate, 4–9 mm long, acute; corolla yellow, 5-lobate, the lobes oblong obovate, ca. 1 cm long, the apex obtuse to emarginate, pubescent on the outer surface and on the upper edge of the inner with both simple and glandular hairs, prominently 5- to 9-nerved; stamens 3, the filaments free, 2–3 mm long, the anthers 3, thecas flexuous, connate, forming an irregular head, ultimately free. *Pistillate flowers* solitary, axillary; peduncle 5–10 cm long, slender, pubescent, bearing a minute subbasal bract; calyx and corolla similar to those of the staminate flower; ovary fusiform, rostrate, tuberculate, pubescent, the styles 3, connate, 2–3 mm long, the stigmas 3, each 2-lobate. *Fruit* bright orange red, ovoid to fusiform, long rostrate, 4–8 cm long, 2–4 cm in diameter, the surface with obtuse to acute tubercles, glabrate, 3-carpellate, 3-valvate, the valves curling back to expose the bright red aril surrounding each seed; seeds numerous in each carpel, oblong, 8–10 mm long, 4–6 mm wide, moderately compressed, slightly 3-toothed at both ends, the testa rugulose.

Widespread in the tropics and subtropics of both the Old and New World. In Panama it is known from every province except for Herrera and Colón, but doubtlessly it also occurs there. It is found in forests and disturbed sites at lower elevations.

The bright red aril surrounding the seeds of the mature fruits is sometimes

[12] For a list of synonyms, see Cogniaux and Harms (1924). Only the above name has been used for Panamanian material.

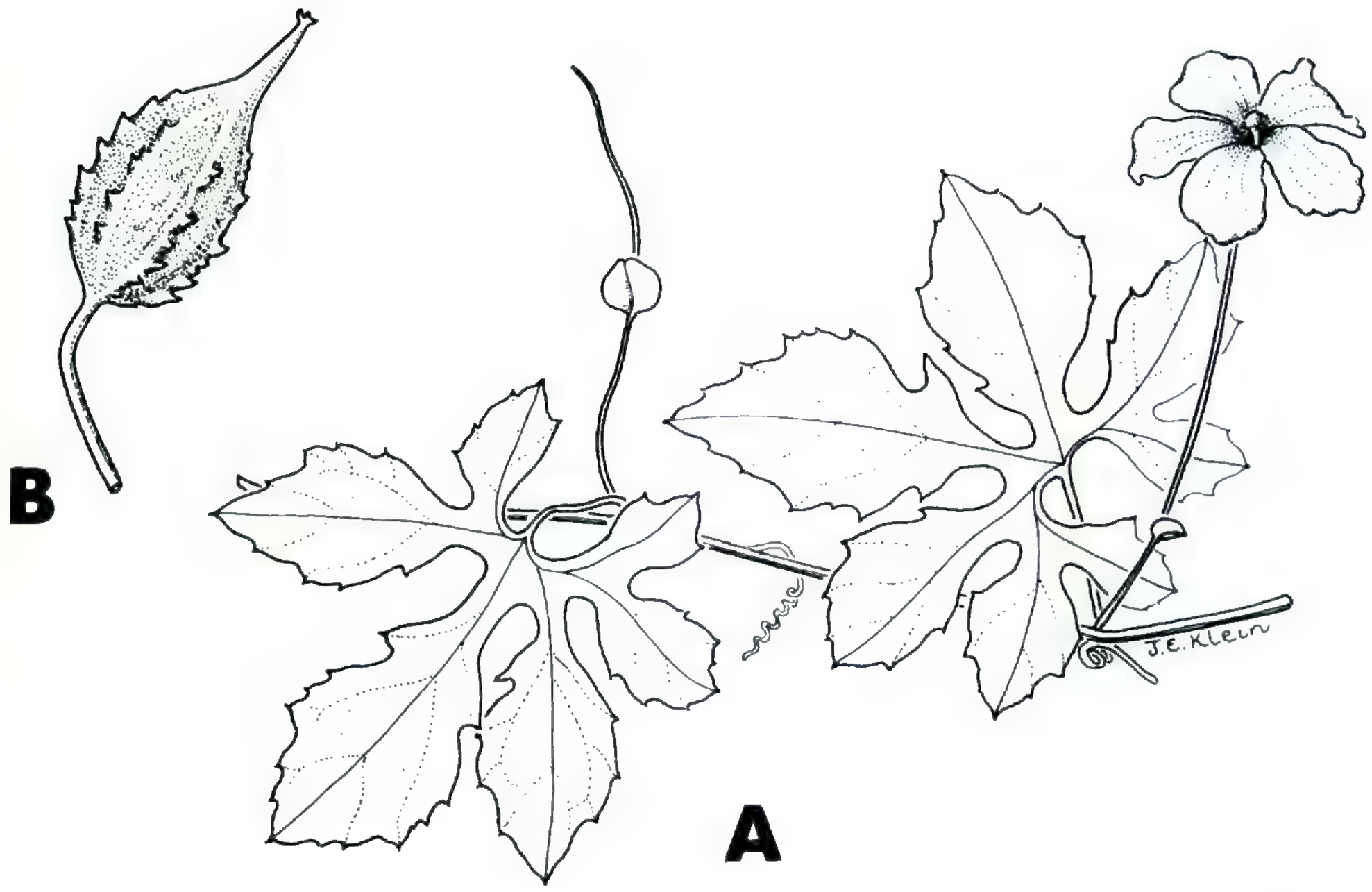


FIGURE 14. *Momordica charantia* L.—A. Habit (×9/10). [After *McDaniel 5181*].—B. Fruit (×9/10). [After *Busey* 543].

eaten by children, the green fruits are cooked, or the leaves parboiled and eaten as a vegetable. The leaves and fruits are also sometimes variously used medicinally for colic, worms, or to induce vomiting. Parts of the plant are reputedly poisonous to humans.

In Panama, the plant is known as "balsamina."

BOCAS DEL TORO: Hill above railroad station at Milla ?, *Croat & Porter 16391* (MO). 5 mi N of Changuinola on the Changuinola River, *Lazor et al. 2472* (FSU). Changuinola to 5 mi S at junction of Río Changuinola and Río Teribe, *Lewis et al. 904* (GH, MO). Chiriquicito to 5 mi S along Río Guarumo, *Lewis et al. 1975* (GH, MO). Without definite locality, *Wedel 224* (MO). CANAL ZONE: Juan Mina, *Bartlett & Lasser 16535* (DUKE, MO). Cerro Viejo on K16C, *Blum 1257* (FSU, NY). Hills near drop zone, few miles from Vernado Beach, *Correa & Gonzales 508* (AA, DUKE, MO). Monkey Hill, *Cowell 26* (NY). Highway between Madden Dam and Boy Scout Road, *Croat 8980* (MO). Corrosion Laboratory near Miraflores Locks, *Duke 4429* (GH, MO). Miraflores Locks, *Dwyer 1006* (MO, US). Military Road K-9, *Ebinger 539* (MO). Near Gatún Dam, *Foster & Chong 1354* (DUKE). Ancón, *Greenman & Greenman 5044* (MO, USF). Las Cruces Trail, *Hunter & Allen 713* (MO). Near Gamboa, Río Mandinga ca. 1 mi up from the canal, *Kennedy et al. 2383* (F). Ancón Hill, *Killip 3039* (GH, NY, US), *3288* (US). Panamerican Highway 2 mi E of Arraijan, *Lewis et al. 5186* (MO). Thunder Hill, Curundu, *McDaniel 5181* (MO). Culebra, *Pittier 2190* (F, NY, US). Balboa, *Standley 3211* (US). Sosa Hill, Balboa, *Standley 25233* (US). Las Cascadas Plantation near Summit, *Standley 25820* (US). Gamboa, *Standley 28436* (US). Río Pedro Miguel, near East Paraiso, *Standley 29925* (US). Corrosion Laboratory near Miraflores Locks, *Stern et al. 64* (GH, MO, US). Near Survival School, Curundu, *Tyson 1057* (FSU, MO). Howard Air Force Base near Red Devil Drop Zone, *Tyson 1856* (MO). Vernado Beach, Point Brujas, near Fort Kobbe, *Welch 19846* (MO). Scrubby forested hills ca. 1 mi SW of Cocoli in the Rodman Naval Ammunition Depot, *Wilbur et al. 12952* (DUKE). Madden Lake, various trails beyond dam, *Witherspoon & Witherspoon 8800* (MO). BARRO COLORADO ISLAND: *Croat 6373* (MO); *Luteyn 774* (DUKE); *Shattuck 1111* (F); *Starry 251* (F). CHIRIQUÍ: San Bartolo Limite, 20 km W of Puerto Armuelles, *Busey 543* (MO). Monte Verde,

2.5 km W of Puerto Armuelles, *Liesner 47* (DUKE, MO). Quebrada Tuco, 9 mi S of Puerto Armuelles, *Liesner 168* (MO). Puerto Armuelles, *Woodson & Schery 822* (GH, MO, US). COCLÉ: Río Hato Airstrip, *Burch 1143* (F, GH, MO, NY). 12 mi NE of Penonomé, *Lewis et al. 1514* (GH, MO, US). Boca del Toabre at confluence of Río Toabre and Río Cocle del Norte, *Lewis et al. 5534* (MO). Between Aguadulce and Antón, *Woodson et al. 1219* (F, GH, MO, NY). DARIÉN: Road to Pinogana from El Real, *Croat 15558* (MO). El Real, Río Tuira, *Duke 5054* (GH, MO, US). Patino, *Duke 10527* (MO). Near Yaviza, *Gentry & Mori 13521* (USF). Village of Mannene, *Kirkbride & Bristan 1616* (MO). ½ mi E of airstrip at El Real, *Lazor & Correa 3394* (FSU). Without other locality, *Macbride 2675* (F). El Real, Río Tuira, *Stern et al. 787* (GH, MO, US). Tucutí, *Terry & Terry 1408* (F, GH, MO). 1 mi N of Río Sabana, *Tyson et al. 4799* (FSU). LOS SANTOS: 7 mi S of Chitré, *Croat 9708* (DUKE, F, GH, MO); *D'Arcy & Croat 4175* (MO). Río Tonosí, vicinity of Tonosí, *Lewis et al. 1541* (GH, MO). Between Tonosí and Macaracas, *Oliver et al. 3571* (MO). Weedy banana grove 2 mi S of Guarare, *Wilbur et al. 12173* (DUKE). PANAMÁ: Pacora, *Carrera 32* (MO). Cerro Campana, *Castillo 15* (DUKE, MO). Along trail between Río Maje and Quebrada Brava, *Croat 34604A* (MO). Panamerican Highway near Jenine, Río Canita, *Duke 3830* (DUKE, GH, MO). Airstrip near beach in Panama City, *Duke 4009* (MO). Entrada de Chame, *Duran 49* (GH). Cermeno, *Dwyer & Robyns 96* (MO). Orillas del Chagres a 50 m de la carretera Transistmica, *Falcon 11* (MO). Dam site near Río Bayano beyond Cañita, *Gentry & Tyson 1682* (MO). Tocumen, *Gonzalez 20* (MO). Vicinity of Arenosa, lower Río Trinidad, *Seibert 605* (GH, MO, NY). Taboga Island, *Standley 27041* (US). Macapale Island in Madden Lake, *Tyson 5488* (FSU, MO). Between Chepo and La Capatina, *Tyson 6754* (MO). Marsh area 2 mi S of Tocumen Airport, *Tyson & Clewell 5896* (DUKE). Weedy roadsides within 1 mi of Chepo, *Wilbur & Luteyn 11801* (DUKE). SAN BLAS: Sasardí, *Duke 10132* (MO). Puerto Obaldía, *Gentry 1567* (MO). VERAGUAS: Puerto Mutis, 12 mi S of Santiago, *Tyson 6016* (FSU, MO).

15. POLYCLATHRA

Polyclathra Bertol., Novi Comment. Acad. Sci. Inst. Bononiensis 4: 438. 1840. TYPE: *P. cucumerina* Bertol.

Pittiera Cogn. in Th. Durand & Pittier, Bull. Soc. Bot. Belg. 30: 271. 1892. TYPE: *P. longipedunculata* Cogn.

Roseanthus Cogn., Contr. U.S. Natl. Herb. 3: 578. 1896. TYPE: *R. albiflorus* Cogn.

Monoecious tendriled *vines*; stems 5- to 10-sulcate. *Leaves* petiolate, simple or foliolate; tendrils mostly 4-branched. *Staminate flowers* solitary in the axils of the leaves, long pedunculate; calyx funnelform or narrowly campanulate, 5-lobate; corolla white, 5-lobate, spreading; stamens 3, inserted on the calyx tube wall, the filaments free, slender, the anthers longitudinally triplicate, connate, one anther unilocular, the other anthers bilocular. *Pistillate flowers* solitary, arising from separate or the same axils as the staminate flowers, short pedunculate; calyx as in the staminate flowers, but shorter; corolla as in the staminate flowers; ovary ellipsoid to globose, 3-carpellate, the styles solitary, slender, the stigmas 3, bilobate. *Fruit* ellipsoidal or oblong, the dry, thin pericarp splitting from the apex and revealing tiers of horizontal cavities, each containing a single seed; seeds numerous, dull brown, horizontal, broadly ovate, compressed, slightly roughened.

Polyclathra is a small, poorly understood genus of Mexico and Central America. Jeffrey (1971) was the first to consider *Roseanthus* and *Pittiera* as congeneric with *Polyclathra* and recognized a possible nine species although he indicated that this number perhaps should be greatly reduced. Dieterle (1976) considered the genus to consist of a single polymorphic species which is the view taken here.

Literature:

Dieterle, J. V. A. 1976. Cucurbitaceae *in* Flora of Guatemala, Fieldiana, Botany 24(11): 306–395.
Jeffrey, C. 1971. Further notes on Cucurbitaceae. II. The tribe Cucurbiteae. Kew Bull. 25: 191–236.

1. **Polyclathra cucumerina** Bertol., Novi Comment. Acad. Sci. Inst. Bononiensis 4: 438. 1840. TYPE: Guatemala, *Vellasquez* (BOLO, holotype, not seen). —FIG. 15.

Cayaponia grandiflora Cogn. in DC., Monogr. Phan. 3: 779. 1881. TYPE: Mexico, *Schott 680* (BM, holotype, not seen).
Pittiera longipedunculata Cogn., Bull. Soc. Bot. Belg. 30: 271. 1892. TYPE: Costa Rica, *Tonduz 3200* (BR, holotype, not seen; US, isotype).
P. trilobata Cogn. in Coult., Bot. Gaz. (Crawfordsville) 20: 289. 1895. TYPE: Guatemala, *Heyde & Lux 4189* (US, holotype, not seen; K, isotype, not seen).
Roseanthus albiflorus Cogn., Contr. U.S. Natl. Herb. 3: 578. 1896. TYPE: Mexico, *Palmer 599* (US, holotype, not seen).
Pittiera grandiflora (Cogn.) Cogn. ex Rose, Contr. U.S. Natl. Herb. 5: 123. 1897.
P. parviflora Cogn. & Rose ex Rose, Contr. U.S. Natl. Herb. 5: 123. 1897. TYPE: Guatemala, *Nelson 3532* (US, holotype, not seen).
Roseanthus elongatus Rose, Contr. U.S. Natl. Herb. 8: 337. 1905. TYPE: Mexico, *Brandegee* (US, holotype, not seen).
R. heterophyllus T.S. Brandegee, Univ. Calif. Publ. Bot. 10: 188. 1922. TYPE: Mexico, *Purpus 8685* (UC, holotype, not seen).
Polyclathra longipedunculata (Cogn.) Jeffrey, Kew Bull. 25: 196. 1971.
P. albiflora (Cogn.) Jeffrey, Kew Bull. 25: 197. 1971.
P. grandiflora (Cogn.) Jeffrey, Kew Bull. 25: 197. 1971.

Slender *vines*; stems glandular pubescent, pilosulous, or glabrate. *Leaves* simple, rounded cordate to ovate, 4–12 cm long and nearly as wide, slightly angulate to deeply 3- to 5-lobate, cordate at the base, the apex of the lobes obtuse, the margins denticulate, chartaceous, the upper and the lower surfaces puberulent or scabrous; petiole 2–8 cm long, slender, pubescent or scabrous; tendrils 4-branched. *Staminate flowers* solitary, axillary; peduncles 7–25 cm long, glandular pubescent; calyx cylindrical, dilated at the apex, greenish white, glandular puberulent, the lobes linear, 8–18 mm long; corolla white, the lobes 2.0–2.5 cm long, obovate oblong, obtuse or acute, the outer surface glandular puberulent; stamens ca. 2 cm long, the anthers forming a cylindrical oblong head, subequalling the filaments, the filaments pilose at the base. *Pistillate flowers* solitary, axillary; peduncles 0.5–1.5 cm long; calyx and corolla as in the staminate flowers; ovary ellipsoid to subglobose, pubescent. *Fruit* green with white stripes, yellowing in age, 4–6(–8) cm long, 3–4 cm wide, ellipsoid to oblong, the thin pericarp splitting from the apex and revealing tiers of horizontal cavities, each containing a single seed; seeds dull brown, ca. 6 mm long, broadly ovate, compressed.

This species ranges from Mexico south to Panama occurring in dry to mesic thickets at low elevations. It is known from Coclé, Panama, and Darién provinces, but probably occurs elsewhere.

COCLÉ: Between Paso del Arado and Ola, *Pittier 5012* (US). DARIÉN: Sambu River, *Pittier 5538* (US). PANAMÁ: Juan Diaz, *Standley 30557* (US).

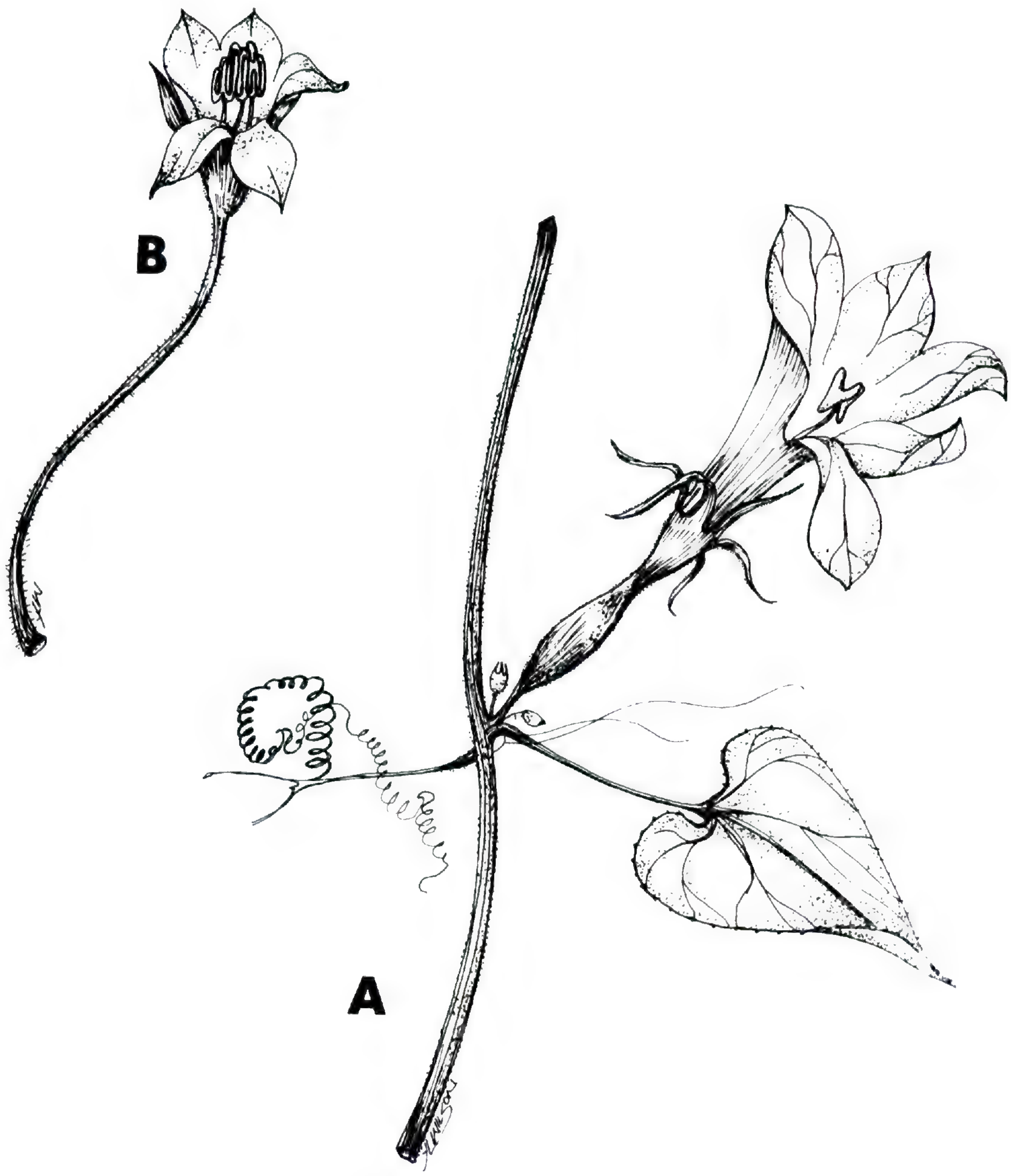


FIGURE 15. *Polyclathra cucumberina* Bertol.—A. Habit and pistillate flower (×⅘). [After *Williams & Molina 42336*—Nicaragua].—B. Staminate flower (×⅘). [After *Tonduz 1473*—Costa Rica].

16. POSADAEA

Posadaea Cogn., Bull. Acad. Roy. Sci. Belgique, sér. 3. 20: 476. 1890. TYPE: *P. sphaerocarpa* Cogn.

Monoecious, tendriled *vines*; stems 5-sulcate. *Leaves* petiolate, simple, 3- to 5-angulate or -lobate; tendrils simple or 2-branched. *Staminate flowers* axillary, short racemose; calyx short campanulate, 5-lobate; corolla 5-parted to the base,

the lobes spreading; stamens 3, free, attached to the hypanthium wall, one unithecous, others bithecous; pistillode cupiform, obscure. *Pistillate flowers* solitary in same axils as the staminate flowers; calyx and corolla as in the staminate flowers; ovary 3-carpellate, the ovary numerous, horizontal; style short, the stigmas 3; staminodia 3, short, ligulate. *Fruits* spherical, indehiscent, pericarp woody, flesh pulpy; seeds narrowly obovate, compressed, smooth.

Posadaea is a monotypic Neotropical genus.

1. **Posadaea sphaerocarpa** Cogn., Bull. Acad. Roy. Sci. Belgique, sér. 3. 20: 477. 1890. TYPE: Colombia, *Posada-Arango* (BR, not seen).—FIG. 16.

Herbaceous *vines*; stems pilose, glabrate in age. *Leaves* with the blades ovate to suborbicular, 3- to 5-angulate or -lobate, 11–15(–18) cm long, 8–14(–19) cm wide, the apex acute to obtuse, the base deeply cordate, the margin remotely denticulate, submembranaceous, both the surfaces sparsely pilose, punctate scabrous in age; petiole 3–9 cm long, sparsely pilose; tendrils simple or 2-branched, pilose. *Staminate flowers* axillary, racemose, the rachis 2–6 cm long, slender, sparsely pilose, 3- to 5-flowered at the apex; pedicels 8–14 mm long, slender, ebracteolate or minutely bibracteolate; calyx campanulate, sparsely villous to glabrate, 6–9 mm long, the lobes 3.0–5.5 mm long, linear, acute, reflexed, sparsely pilose to glabrous; corolla yellow, the lobes obovate oblong, 8–9 mm long, nearly as wide, 7- to 9-nerved, sparsely short villous on both the surfaces; anthers white, 1.5–2.0 mm long, the theca recurved at the apex; pistillode cupulate, minute. *Pistillate flowers* axillary, solitary; peduncle stout, 2–3 cm long, short pilose; calyx and corolla as in the staminate flowers but slightly smaller; ovary elliptic ovoid, ca. 1 cm long, pilose, style ca. 3 mm long, the stigma dilated, obcordate, subreflexed, 3–5 mm wide; staminodia obtuse, 1.5–2.0 mm long. *Fruit* light greenish yellow, globose, 8–10 cm in diameter, the pericarp woody, the flesh pulpy, white, the surface minutely verruculose; peduncle 9–15 cm long, tapering from a slender base to a wide thickened apex and merging with the fruit, glabrous; seeds narrowly obovate, 12–14 mm long, 7–8 mm wide, compressed, white, smooth.

Posadaea sphaerocarpa ranges from Guatemala through Central America south to Colombia, Ecuador, Guiana, Brazil, and Trinidad. It occurs in tropical moist forests and thickets, scrambling over shrubs or on the ground.

The gourdlike fruits resemble those of *Lagenaria* and are reportedly used in a similar manner. In Panama this species is called "brujito."

CANAL ZONE: Valley of Masambi, on the road to Las Cascadas Plantation, *Pittier* 2589 (GH, US). Around Culebra, *Pittier 4805* (US). Las Cascadas Plantation, near Summit, *Standley* 29582 (US). PANAMÁ: Río Tapia, *Standley* 28303 (US).

17. PSIGURIA

Psiguria Neck. ex Arn., J. Bot. (Hooker) 274 3: 247. 1841. LECTOTYPE: *P. pedata* (L.) R.A. Howard.

Anguria Jacq., Enum. Pl. Carib. 9. 1760; non Mill., 1754. LECTOTYPE: *A. pedata* (L.) Jacq.

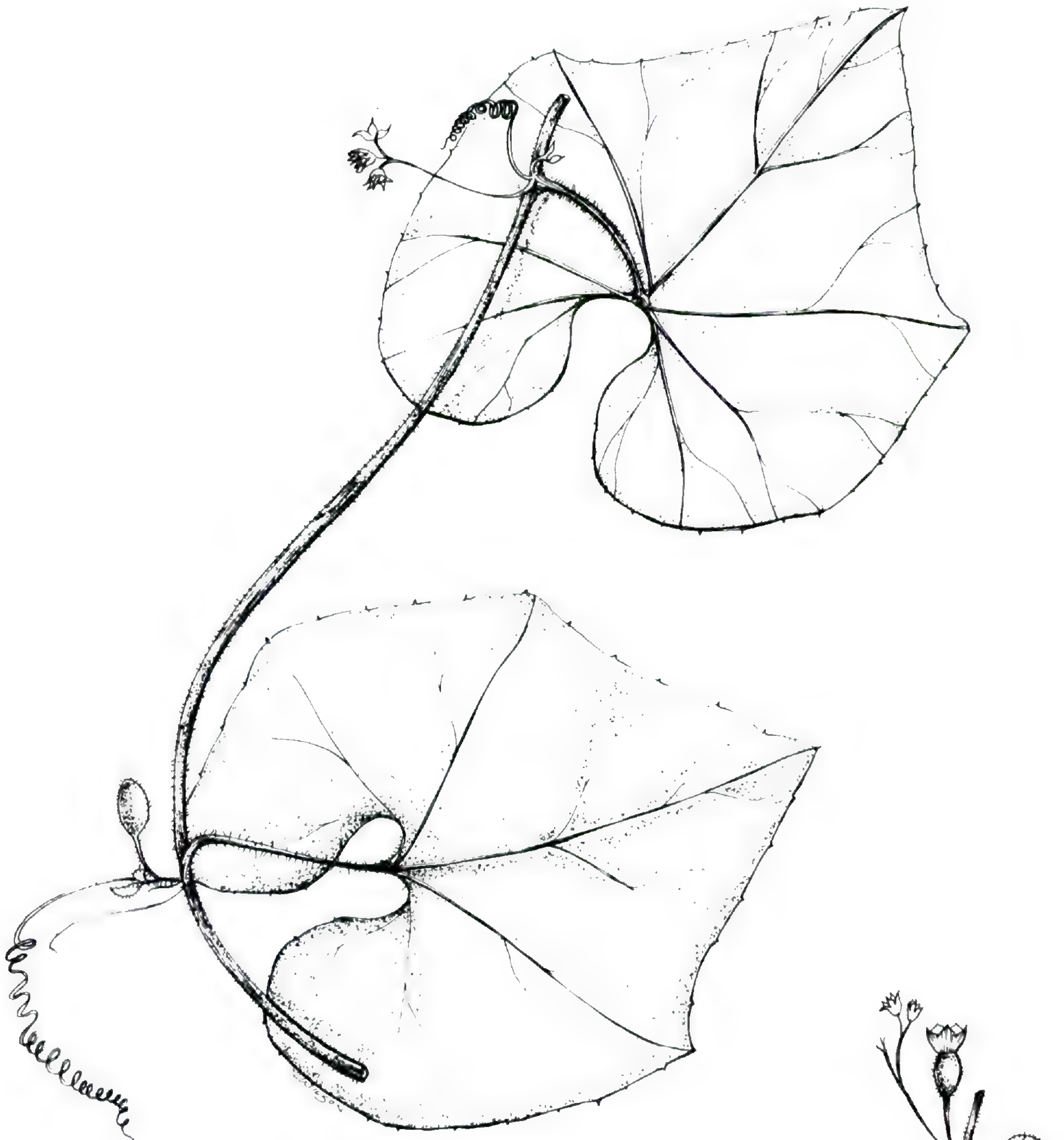


FIGURE 16. *Posadaea sphaerocarpa* Cogn.—A. Habit (×7/10). [After *Standley* 29582 (US)].—B. Flower (×7/10). [After *Skutch* 3965 (US)—Costa Rica].

Dioecious or rarely monoecious, tendriled *vines* or *lianas*; stems 5- to 10-sulcate. *Leaves* petiolate, entire, lobate, or 3- to 5-foliolate; tendrils simple. *Staminate flowers* clustered at the end of long peduncles; calyx elongate cylindric, 5-lobate; corolla rotate, 5-lobate; stamens 2, included, free, the filaments short, the anthers linear or oblong, dorsifixed, bilocular, the theca straight, rarely replicate at the base. *Pistillate flowers* 1–3, short pedunculate; calyx and corolla

as in the staminate flowers; ovary ovoid, 2-carpellate, the ovules numerous, horizontal, the styles connate on most of their length, the stigmas 2-branched; staminodia 2, minute. *Fruits* indehiscent, ovoid to oblong; seeds numerous, oblong, compressed.

Psiguria is a genus of 15–30 species restricted to the American tropics. It is closely allied to *Dieudonnaea*, *Gurania*, and *Guraniopsis* and may eventually prove to be congeneric with one or more of these.

I am following Howard (J. Arnold Arb. 54: 453–470. 1973) in accepting *Psiguria* over the well-known generic name *Anguria*. Many more species in *Anguria* need to be transferred to *Psiguria*, but must await further study of this and the allied genera.

a. Calyx tube cylindrical, green speckled; calyx lobes triangular, conspicuously darker green than the tube ..... 4. *P. warscewiczii*
aa. Calyx tube flask-shaped, solid green; calyx lobes subulate or lanceolate, the same color as the tube.
  b. Leaves coriaceous ..... 1. *P. bignoniacea*
  bb. Leaves membranaceous or chartaceous.
    c. Leaves simple, margins entire or sinuate undulate ..... 2. *P. longipedunculata*
    cc. Leaves 3- to 5-foliolate or deeply 3- to 7-lobate ..... 3. *P. pedata*

1. **Psiguria bignoniacea** (Poepp. & Endlicher) Wunderlin, Phytologia 38: 219. 1978.

Anguria bignoniacea Poepp. & Endlich., Nov. Gen. Sp. Pl. 2: 53. 1838. TYPE: not known.
A. triphylla Miq., Linnaea 19: 136. 1845. TYPE: not known.
A. pachyphylla Donnell Smith, Bot. Gaz. (Crawfordsville) 54: 236. 1912. TYPE: Costa Rica, *Tonduz 11535* (US, holotype).
A. longeracemosa Pittier, J. Wash. Acad. Sci. 19: 185. 1929. TYPE: Panama, *Pittier 6582* (US, holotype; US, isotype).

Dioecious *vines*; stems puberulent at the nodes, otherwise glabrous. *Leaves* 3-foliolate or sometimes simple, the leaflets 9–21 cm long, 6–13 cm wide, the middle leaflet usually slightly larger, elliptic to obovate, the lateral leaflets asymmetrical, sometimes with a lateral lobe, the apex of the leaflets acute to acuminate, the base cuneate to slightly rounded, the margins entire or undulate, coriaceous, the upper surface minutely white pustulate, the lower surface glabrate; petioles 2.5–5.0 cm long, glabrate; tendrils simple, robust, glabrate. *Staminate flowers* axillary, sessile in a subcapitate cluster at the end of a long pedunculate raceme; peduncle 15–25 cm long, glabrate; calyx flask-shaped, 8–11 mm long, the outer surface appressed puberulent, the inner surface sparsely villous, the lobes lanceolate, 2–3 mm long, spreading or reflexed; corolla reddish orange, the lobes obovate, subacute, 4–6 mm long, both the surfaces papillose pubescent; anthers linear, 5–6 mm long, appendix ca. 0.5 mm long, glabrous. *Pistillate flowers* 1–3 in the axils of the leaves, often at the ends of the branches in the axils of the reduced leaves; calyx and corolla as in the staminate flowers; ovary oblong, glabrous, ca. 2 cm long, not sharply differentiated from the calyx tube. *Fruits* green with lighter green stripes, 4–6 cm long, 2.0–2.5 cm in diameter, the base rounded, the apex attenuate; seeds oblong ovate, gray, ca. 7 mm long, ca. 4 mm wide, smooth.

This species occurs from southern Mexico to Peru and Ecuador. It occurs usually in the canopy in moist or wet forests at elevations up to about 1,000 m. The leaves are highly variable with both simple and 3-foliolate forms encountered. In the sterile condition it can be easily confused with *P. warscewiczii*, also a highly variable species. The latter species is usually encountered along streams, the leaves are submembranaceous to chartaceous, and the calyx tube is cylindrical.

BOCAS DEL TORO: Fish Creek Hills, Chiriquí Lagoon, *Wedel 2429* (GH, MO, US). BARRO COLORADO ISLAND: *Croat 8082* (F, MO), *8485* (F, MO, NY), *12218*, *14573*, *16518* (all MO). COCLÉ: Cerro Pilón, El Valle, by weather station, *Duke & Lallathin 15007* (USF). COLÓN: Santa Rita Ridge, 5–6 mi E of Transisthmian Highway, *Lewis et al. 5393* (MO). Santa Rita Ridge Road, 1.9 km from Boyd-Roosevelt Highway, *Mori & Kallunki 1818* (MO). Santa Rita Ridge Road, 6 km from Boyd-Roosevelt Highway, *Mori & Kallunki 5085* (MO, USF). DARIÉN: Summit camp, between Sasardí and Mortí, *Duke 10045* (MO). Forests around Yaviza, *Pittier 6582* (US). Caná and vicinity, *Williams 941* (NY). LOS SANTOS: Loma Prieta, Cerro Grande, *Lewis et al. 2217* (GH, MO, US). PANAMÁ: 1 mi beyond La Eneida, region of Cerro Jefe, *Correa & Dressler 963* (MO). 5–6 mi N of El Llano, near San Blas border, *Gentry 5808* (F, MO). 1–2 mi beyond Goofy Lake, *Gentry & Dwyer 3412* (MO). 6 km above Panamerican Highway on road from El Llano to Cartí-Tupile, *Kennedy 1789a* (MO). El Llano-Cartí Road, 9.6 km from Panamerican Highway, *Mori & Kallunki 1838* (MO). El Llano-Cartí Road, 12.7 km from Panamerican Highway, *Mori & Kallunki 4680* (MO); *Mori et al. 4690* (MO). Along El Llano-Cartí Road, 8 km N of Panamerican Highway at El Llano, *Nee & Warmbrodt 10351* (MO, USF); *Nee et al. 8803* (MO, USF). Cerro Azul, *Porter et al. 4088* (MO). VERAGUAS: Beyond Río Tres Brazos, 11 km beyond Santa Fé, *Croat 25652* (MO).

2. **Psiguria longipedunculata** (Cogn.) Wunderlin, Phytologia 38: 219. 1978.

Anguria longipedunculata Cogn., Mém. Couronnés Mém. Acad. Roy. Sci. Belgique 27: 21. 1876. TYPE: not known.
A. dunlapii Standl., Publ. Field Columbian Mus., Bot. ser. 4: 298. 1929. TYPE: Panama, *Dunlap 490* (F, holotype; F, US, isotypes).

Dioecious *vines*; stems slender, glabrous. *Leaves* simple, 7–12 cm long, 3–5 cm wide, lanceolate to elliptic, the apex acute, the base truncate to rounded, the margin entire, undulate to sinuate lobed, sometimes remotely toothed, membranaceous, the upper surface minutely white pustulate, the lower surface glabrous; petioles 1–3 cm long, glabrous; tendrils simple, slender, glabrous. *Staminate flowers* axillary, sessile in subcapitate clusters at the end of long pedunculate racemes; peduncle 12–15(–40) cm long, glabrous; calyx flask-shaped, 7–11 mm long, glabrous, the lobes lanceolate, ca. 2 mm long, spreading or reflexed; corolla reddish orange, the lobes obovate, subacute, 4–5 mm long; anthers oblong, ca. 4–6 mm long, appendix ca. 0.5 mm long, papillate. *Pistillate flowers* not seen. *Fruits* not seen.

Psiguria longipedunculata is a rare species ranging from Mexico to Panama. It occurs at elevations of 300 to 500 m. In Panama it is known only from the type collection of *Anguria dunlapii*.

BOCAS DEL TORO: Farm 6, Changuinola Valley, *Dunlap 490* (F, US).

3. **Psiguria pedata** (L.) R.A. Howard, J. Arnold Arb. 54: 441. 1973.

Cucumis pedatus L., Syst. Nat. ed. 10. 1279. 1759. TYPE: not known.
Anguria pedata (L.) Jacq., Enum. Pl. Carib. 31. 1790.
A. polyphyllos Schlecht., Linnaea 24: 712. 1851. TYPE: not known.

A. dentata Schlecht., Linnaea 24: 713. 1851. TYPE: not known.
A. affinis Schlecht., Linnaea 24: 760. 1851. TYPE: not known.
A. pedata var. *ottoniana* Sauv., Fl. Cubana 904. 1873. TYPE: not known.
A. pedata var. *polyphyllos* (Schlecht.) Cogn., Mém. Couronnés Mém. Acad. Roy. Sci. Belgique 27: 10. 1876.
A. pedata var. *dentata* (Schlecht.) Cogn., Mém. Couronnés Mém. Acad. Roy. Sci. Belgique 27: 10. 1876.
A. pedata var. *affinis* (Schlecht.) Cogn., Mém. Couronnés Mém. Acad. Roy. Sci. Belgique 27: 10. 1876.

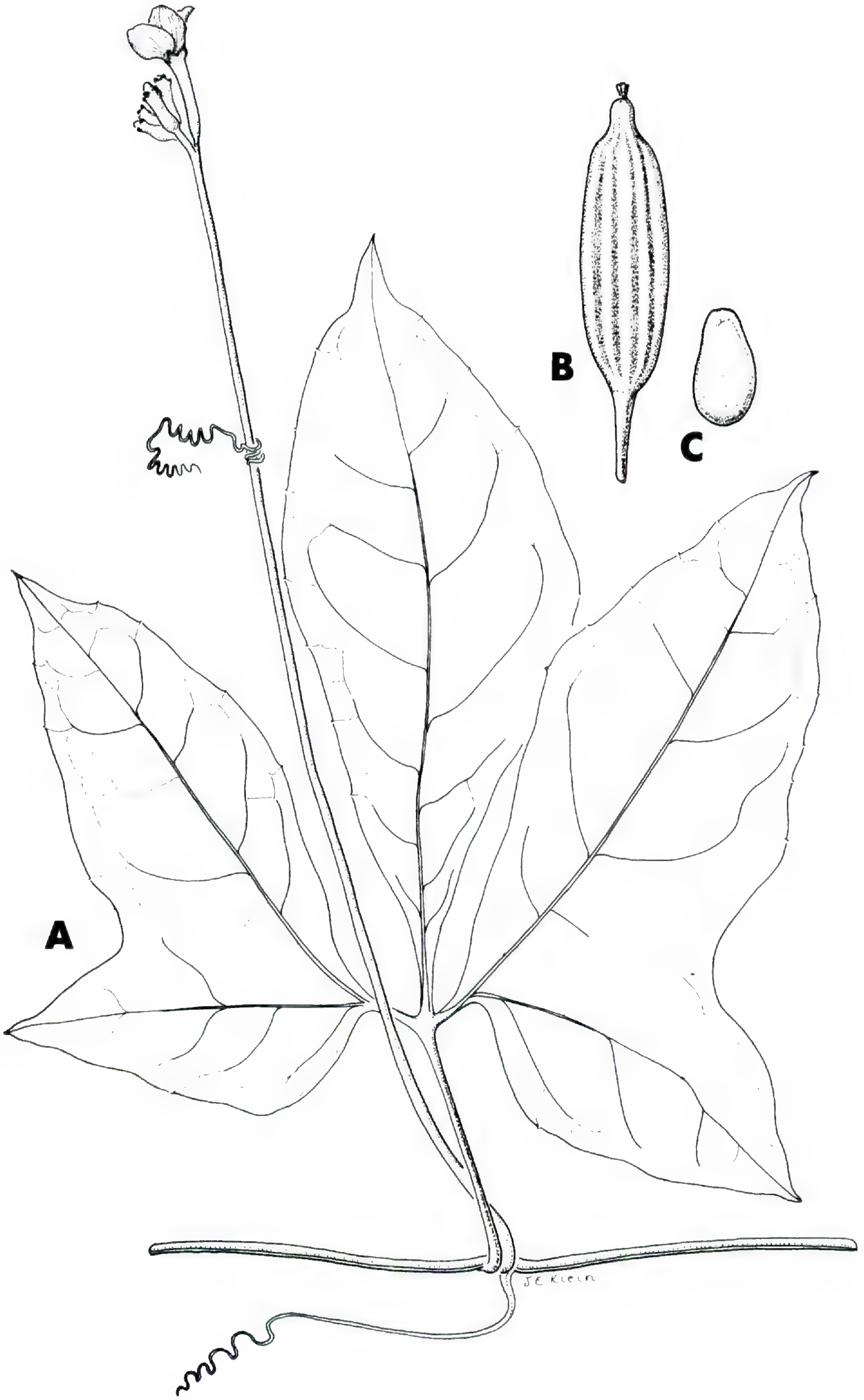
Monoecious *vines*; stems glabrous. *Leaves* 3- to 5-foliolate, 3- to 7-lobate, or sometimes simple, suborbicular, the leaflets or the segments 8–10 cm long, 2–4 cm wide, lanceolate or oblong, the apex acute to obtuse, the base asymmetrical and often auriculate, the margin remotely few toothed, undulate, or entire, submembranaceous to chartaceous, the upper surface minutely white pustulate, the lower surface glabrate; petioles 1–3 cm long, glabrous; tendrils simple, slender, glabrous. *Staminate flowers* axillary in subcapitate clusters at the end of long pedunculate racemes; peduncle 12–20 cm long, glabrous; pedicels 5–16 mm long, glabrous; calyx flask-shaped, 6–8 mm long, glabrous, the lobes triangular, 1–2 mm long, erect, glabrate; corolla orange, the lobes oblong, obtuse, 1.0–1.5 cm long, both the surfaces papillose; anthers oblong, 5–6 mm long, appendix ca. 1 mm long, glabrous. *Pistillate flowers* solitary or in pairs in the axils of the leaves; calyx and corolla as in the staminate flowers; ovary oblong, ca. 1 cm long, glabrous; peduncle 3–5 cm long. *Fruits* green with lighter stripes, ovoid oblong, 3–4 cm long, 1.5–2.0 cm in diameter, the base rounded, the apex rostrate, the flowers often persisting; seeds oblong ovate, gray, ca. 6 mm long, ca. 3 mm wide, smooth.

This species is confined primarily to the Caribbean region. It has been reported from Colombia and Panama by Cogniaux (1916), but no material from these countries has been seen.

4. **Psiguria warscewiczii** (Hook. f.) Wunderlin, Phytologia 38: 219. 1978.

Anguria warscewiczii Hook. f., Bot. Mag. *tab.* 5304. 1862. TYPE: not known.—FIG. 17.

Dioecious *vines*; stems glabrate. *Leaves* 3-foliolate, the leaflets 10–18 cm long, 3–7 cm wide, the middle leaflet usually slightly larger than the lateral leaflets, elliptic, broadest near or above the middle, the lateral leaflets oblique, with a lateral lobe or sometimes divided to the base into two segments, the apex acuminate, the base cuneate or rarely rounded, the margins entire to undulate, submembranaceous to chartaceous, the upper surface minutely white pustulate, the lower surface glabrate, minutely white pustulate, or puberulent, especially on the nerves; petioles 2–7 cm long, robust, glabrous; tendrils simple, robust, glabrous. *Staminate flowers* axillary, subsessile in subcapitate clusters at the end of long pedunculate racemes; peduncle 15–30 cm long, glabrous; calyx cylindrical, 1–2 cm long, glabrate on the outer surface, puberulent within, the lobes triangular, 2–3 mm long, spreading; corolla reddish orange, the lobes ovate oblong to suborbicular, acute or rounded, 5–7 mm long, both the surfaces papillose pubescent; anthers oblong, 5–6 mm long, the appendix ca. 0.5 mm long, glabrous. *Pistillate flowers* axillary, 1–3; calyx and corolla as in the staminate flowers;


B
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ovary oblong fusiform, glabrous; peduncles 3–4 cm long. *Fruits* dark green with lighter green or whitish stripes, oblong, 5.5–7.0 cm long, 1.8–2.5 cm in diameter, the base cuneate, the apex rostrate, the flower often persisting; seeds irregularly ovate elliptic, tan, 7–9 mm long, 4–6 mm wide, smooth.

Psiguria warscewiczii is a relatively common and variable species of tropical wet forests of southern Mexico south to Peru. It resembles *P. bignoniacea*, but differs in the characters given in the discussion of that species.

BOCAS DEL TORO: Changuinola Valley, *Dunlap 446* (F). CANAL ZONE: Madden Dam, *Allen 2011* (MO). Río Providencia, 12 mi S of Colón, *Blum & Tyson 2328* (MO). Near Paraíso, *Croat 7158* (MO). N of Summit Garden, *Croat 12327* (MO). Between Margarita and Gatún, *Croat & Porter 15375* (MO). Military Road K-9, *Ebinger 540* (MO). Boy Scout Camp Road, *Gentry 5505* (MO). Road between Transisthmian Highway and Madden Dam, *Gentry 6740* (F, MO). Farfan Beach, from Thatcher Highway to Palo Seco, *Lewis et al. 57* (GH, MO, US). Fort Kobbe Military Reservation, *Luteyn 1073* (DUKE). Navy Reservation N of Gamboa, *Maas & Dressler 713* (MO). Railroad relocation between Gorgona and Gatún, *Pittier 2283* (US). Around Gamboa, *Pittier 3701* (US). Around Tabernilla, *Pittier 3820* (US). Upper Chilibre River, ½ mi below Chilibre, *Seibert 1508* (US). Balboa, *Standley 25450, 29271* (both US). Obispo, *Standley 31728* (US). Pedro Miguel, *White 133* (MO). BARRO COLORADO ISLAND: *Aviles 902, 919, 995* (all F); *Bailey & Bailey 150, 289* (both F); *Bangham 537* (F, GH); *Croat 4571* (F, MO), *5901, 6583, 7469* (all MO), *8499* (F, MO), *9435, 10850, 11663, 14858, 16524* (all MO); *Ebinger 162* (F, MO, US), *641* (F, MO); *Foster 834* (DUKE); *Kenoyer 567* (US); *Luteyn & Croat 915* (DUKE); *Shattuck 163* (F, MO), *269* (F, GH), *564* (F, US), *641* (MO), *652* (F); *Standley 31257, 40921* (both US); *Starry 45, 220, 303* (all F); *Salvoza 961* (F); *Wetmore & Abbe 32* (F, GH); *Wilbur & Weaver 10806* (DUKE); *Zetek 4557* (F, MO). CHIRIQUÍ: Quebrada Caña Blanca, Burica Peninsula, *Croat 22583* (F, MO, NY, US). San Bartolo Arriba W of Puerto Armuelles, *Croat 26708* (MO). COCLÉ: El Valle de Antón, *Alston 8788* (US). 12 mi NE of Penonomé, *Lewis et al. 1521* (GH, MO). COLÓN: 0.5 km from the Río Buenaventura, near Portobelo, *Kennedy & Gra 2237* (MO, US). Río Guanche, 3–4 km above bridge on road to Portobelo, *Witherspoon & Witherspoon 8637* (MO). DARIÉN: El Real, *Allen 952* (F, GH, MO, US). El Río Aruza, *Bristan 1361* (MO). Río Pirre, *Croat & Porter 15539* (MO). Road from El Real to Pinogana, *Duke 4888* (GH, MO, US), *5146, 5147* (both GH, MO). 10 mi S of El Real on Río Pirre, *Duke 5438* (MO). Cerro Piriaque, *Duke 8112* (MO). Trail from Río Pucro to Quebrada Maskia, *Duke 13072* (MO). El Real, 1–3 km S of town, *Gentry 13461* (USF). Río Pirre near town of Pirre, *Gentry & Clewell 6935* (MO). Panamerican Highway between Pinogana and Yaviza, 1 km from Tuira, *Stern et al. 134A* (MO). Río Tuira, along trail to Río Pirre, *Stern et al. 298* (GH, MO, US). Paya, Río Payo, along trail between Paya and Pucro, *Stern et al. 414* (GH, MO, US). Cerro Piriaque, *Tyson et al. 3820* (MO). LOS SANTOS: Loma Prieta, *Duke 11851* (MO). PANAMÁ: Panama City, at Lefevre Park, *Bartlett & Lasser 16336* (MICH). Río Chagres, 1 mi above Madden Lake, *Duke 4485* (GH, MO, US). Panamerican Highway halfway between El Llano and Río Mamoní, *Duke 5535* (MO, US). Near top of Cerro Campana, *Duke 5961* (MO). Tocumen, *Dwyer 4402* (FSU). Goofy Lake, *Dwyer 7112* (MO, USF). 1 km E of El Llano, *Gentry 6462* (F, MO). Camino de las Sabinas, *Heriberto 265* (US). 6 km above Panamerican Highway on road from El Llano to Cartí-Tupile, *Kennedy 1789b* (MO). Campana, *Lewis et al. 3163* (MO). Tributary of Río Chagres, 5 mi SW of Cerro Brewster, *Lewis et al. 3389* (MO). Road to Cerro Campana 2–4 mi above the Interamerican Highway, *Luteyn 3996* (DUKE). Carretera Transistmica at the continental divide, Alcade Diaz, *Nee 8304* (MO, USF). Sabanas Railroad, NE of Panama City, *Paul 172* (US). Sabana de Juan Corso, near Chepo, *Pittier 4541* (US). Agricultural Station Matías Hernández, *Pittier 6765* (US). Between Panamá and Sabanas, *Riley 113* (MO, US). Along Corozal Road, *Standley 26848* (US). 5 mi E of Cañita and 23 mi E of Chepo, *Tyson & Smith 4154* (FSU, MO, SCZ). VERAGUAS: 3–5 mi N of Santa Fé, *Gentry 3010* (MO).

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FIGURE 17. *Psiguria warscewiczii* (Hook. f.) Wunderlin.—A. Habit (×¾).—B. Fruit (×¾).—C. Seed (×2¼). [After *Croat 4571*].

18. RYTIDOSTYLIS

Rytidostylis Hook. & Arn., Bot. Beech. Voy. 424. 1840. TYPE: *R. gracilis* Hook. & Arn.

Elaterium Jacq., Enum. Pl. Carib., Vol. 9. 1760; non Mill., 1754. TYPE: *E. carthaginense* Jacq.

Monoecious, tendriled *vines*; stems 5-sulcate. *Leaves* alternate, petiolate, simple, entire or lobate; tendrils simple or 2- to 3-branched. *Staminate flowers* green, white, or yellow, inflorescences few-to-many-flowered, umbelloid pedunculate or fasciculate, axillary clusters; calyx elongate cylindric, 5-lobate; corolla (4–)5-lobate; stamens 3, the filaments connate, the anthers connate in an oblong or globose head, the theca flexuous, 2-locular. *Pistillate flowers* solitary; calyx and corolla as in the staminate flowers; styles 3, connate; ovary obliquely ovoid, hispid or echinate, 1- to 6-locular, usually 3-locular with 1 locule aborted, the ovules erect, ascending, or horizontal. *Fruit* obliquely ovoid to subglobose, gibbous, rostrate or not, elastically dehiscent; seeds elliptical to ovate compressed.

Rytidostylis is a genus consisting of perhaps a half dozen species occurring in the Neotropics. Numerous poorly delimited species have been described. The genus is much in the need of revision.

See Jeffrey (1962) for a discussion of the name *Rytidostylis* over the much better known *Elaterium*.

The Panamanian material is interpreted as belonging to a single, highly polymorphic, widespread species. However, further revisionary study may eventually result in the recognition of additional taxa for Panama, perhaps adding names to the present synonymy.

1. **Rytidostylis carthaginensis** (Jacq.) Kuntze, Rev. Gen. Pl. 1: 258. 1891.—FIG. 18.

Elaterium carthaginense Jacq., Enum. Pl. Carib. 31. 1760; Sel. Stirp. Amer. 241. *tab.* 54. 1763.
Rytidostylis gracilis Hook. & Arn., Bot. Beech. Voy. 424. 1841. TYPE: not known.
Elaterium cordatum Hook. f., Trans. Linn. Soc. London 20: 224. 1851. TYPE: not known.
E. ciliatum Cogn., Mém. Couronnés Mém. Acad. Roy. Sci. Belgique 28: 54. 1877. TYPE: not known.
E. gracile (Hook. & Arn.) Cogn., Mém. Couronnés Mém. Acad. Roy. Sci. Belgique 28: 51. 1877.
E. longiflorum Cogn., Mém. Couronnés Mém. Acad. Roy. Sci. Belgique 28: 54. 1877. TYPE: not known.
E. ciliatum var. *major* Cogn., Mém. Couronnés Mém. Acad. Roy. Sci. Belgique 28: 54. 1877. TYPE: not known.
Rytidostylis ciliata (Cogn.) Kuntze, Rev. Gen. Pl. 1: 258. 1891.
R. cordata (Hook. f.) Kuntze, Rev. Gen. Pl. 1: 258. 1891.
Tytidostylis longiflora (Cogn.) Kuntze, Rev. Gen. Pl. 1: 258. 1891.
Elaterium carthaginense var. *cordatum* (Hook. f.) Svens., Amer. J. Bot. 22: 256. 1935.
E. macrophyllum Standley & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23: 94. 1944. TYPE: Guatemala, *Tuerckheim 1728* (F, not seen).
Rytidostylis macrophyllus (Standley & Steyerm.) Dieterle, Fieldiana, Bot. 24(11): 373. 1976.

Vines; stems, pubescent to glabrate. *Leaves* cordate to suborbicular, 6–8(–12) cm long, 5–7(–9) cm wide, entire, 3- to 5-angulate, or 3- to 5-lobate, the apex of the lobes acute to acuminate, the base cordate, minutely and remotely to con-

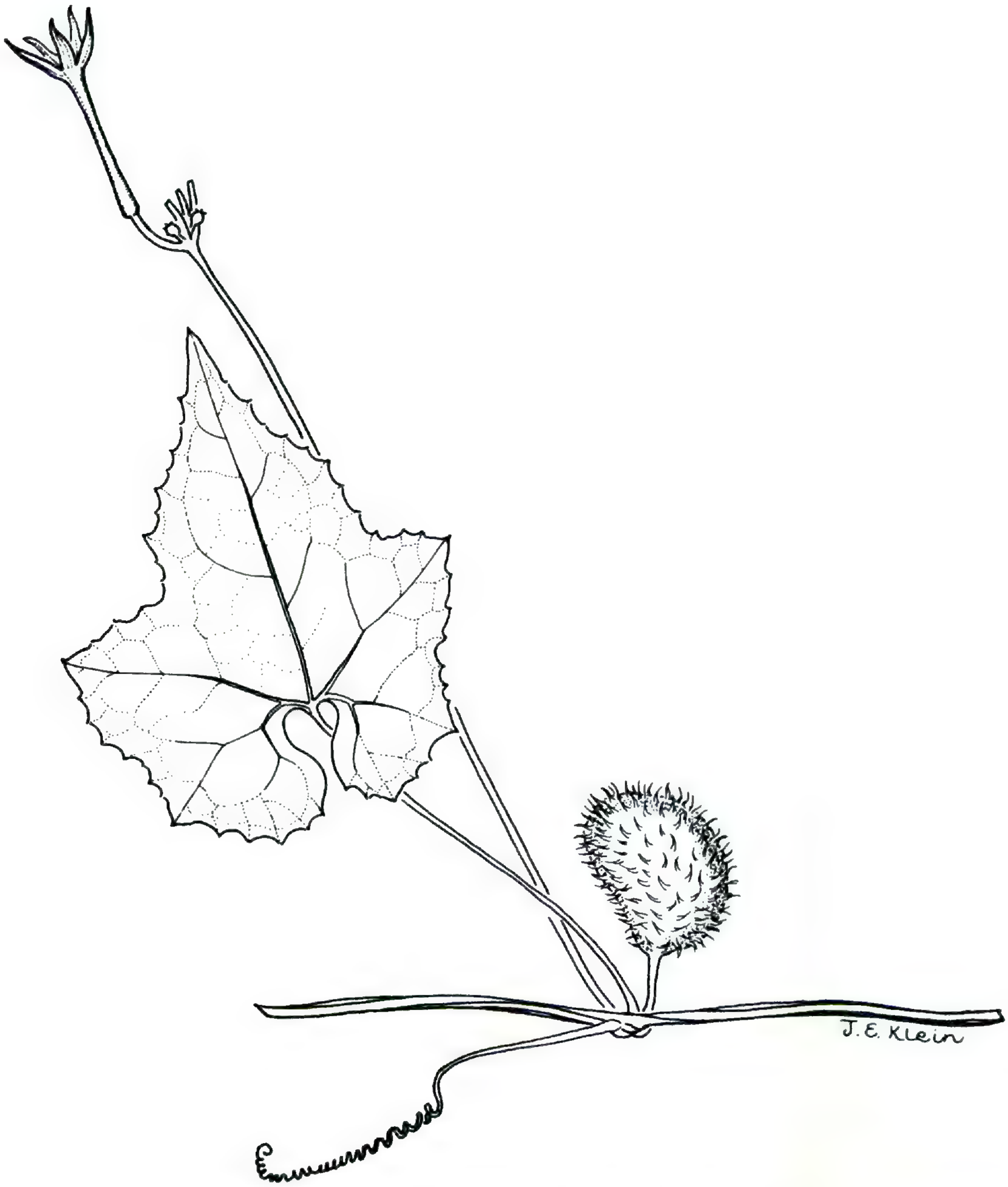

FIGURE 18. *Rytidostylis carthaginensis* (Jacq.) Kuntze. Habit (×1). [After *Tyson & Dwyer 1200*].

spicuously dentate, submembranaceous to chartaceous, the upper surface scabrous on the veins, minutely pustulate; petioles 1–6 cm long, pubescent to glabrate; tendrils 2- to 3-branched, rarely simple, puberulent to glabrate. *Staminate inflorescences* axillary, long pedunculate to subsessile subumbelloid racemes, the rachis (if well developed) slender, to 20 cm long; pedicels filiform, 3–8 mm long. *Staminate flowers* greenish, white, or yellow; calyx tube elongate cylindric, 2–3 cm long, the lobes ca. 1 mm long, setose, glabrate; corolla lobes lanceolate or linear lanceolate, acuminate, spreading, the outer surface glabrous, the inner

surface densely papillose; stamens subequalling the calyx tube, the filaments filiform, connate, glandular papillose at the base, sparsely villous to glabrate toward the middle, glabrous at the apex, the staminal column truncate or subcapitate at the apex. *Pistillate flowers* solitary, axillary, subsessile or with the peduncle to 1 cm long, the calyx and the corolla as in the staminate flowers; ovary obliquely ovoid, echinate, the ovules ascending, the styles slightly shorter than the hypanthium tube, densely papillose on the lower half, the stigmas connate, forming an oblong capitate head. *Fruits* green, obliquely ovoid, slightly compressed, 2.0–4.0 cm long, 1.2–2.0 cm wide, with bristles to 5 mm long, elastically dehiscent; seeds 12–16, tan, broadly ovate, 6–10 mm long, 5–8 mm wide, compressed, winged marginally on the lower ⅔, 3-dentate at the apex.

This species ranges from southern Mexico south to Venezuela, Colombia, Ecuador, Brazil, and Peru. In Panama it occurs in open woods and disturbed sites at elevations up to 2,000 m.

In Panama this plant is known as "gallotillo," "norbo cimarron," or "naibe wagedu." In Guatemala it is called "cochinito," "quiamul," or "sandia de raton." In some regions the young fruits are cooked and eaten as a vegetable.

BOCAS DEL TORO: Róbalo Trail, N slopes of Cerro Horqueta, *Allen 4933* (MO). Río Teribe, near Quebrada Lukulon, *Kirkbride & Duke 509* (MO). 10–15 mi inland (S) from mouth of Changuinola River, *Lewis et al. 894* (GH, US), *4253* (MO). CANAL ZONE: Vicinity of Summit Golf and Country Club, *Croat 12267* (MO, SCZ), *12793* (F, GH, MO, NY, USF). Madden Forest Road at entrance to Boy Scout Road, *Croat 12896* (MO). Panamerican Highway near La Chorrera, *D'Arcy 9457*, *9471* (both MO). Rodman Ammunition Depot, *Foster 1488* (DUKE, F). Road K-9, 2 mi from W border of Zone to cleared area near Canal, *Gentry 1780* (DUKE, GH, MO). Road between Transisthmian Highway and Madden Dam, *Gentry 6741* (MO). C-29 beyond Summit, *Harvey 5214* (F). Along K-2, Contractors Hill, *Lewis et al. 2877* (MO). Near entrance to Boy Scout Camp 1.6 km from Madden Dam Road, *Mori et al. 4033* (MO, USF). Abandoned road C-29, 6 km E of Gamboa, *Nee 9050* (MO, USF). Culebra, *Pittier 2156* (US). Gamboa, *Pittier 4437* (US). Balboa, *Standley 25436*, *25599* (both US). Las Cascacadas Plantation, near Summit, *Standley 25821* (US). Balboa, *Standley 29284* (US). Boy Scout Road near Madden Dam, *Tyson & Dwyer 1200* (FSU, MO). CHIRIQUÍ: Boquete, *D'Arcy & D'Arcy 6456* (MO). Bajo Chorro near Boquete, *Davidson 430* (F, MO, US). Cerro Horqueta, NW of Boquete, *Dwyer et al. 466* (MO). Vicinity of Boquete, *Lewis et al. 384* (DUKE, GH, MO, US); *Maurice 716* (MO, US); *Maxon 4997* (US); *Pittier 3153* (US). 2 mi SW of Guabala, *Tyson et al. 4253* (DUKE). COCLÉ: 39 km from Panamerican Highway along road to El Valle de Antón, *Correa 322* (MO). Between Cerro Pilón and El Valle de Antón, *Duke & Dwyer 13906* (MO). Capellania, Natá, *Gonzalez 48* (DUKE). Olá, *Pittier 5029* (NY, US). W slope and summit of Cerro Valle Chiquito, *Seibert 501* (GH, MO, NY). 1–5 mi S of Antón, *Tyson & Blum 2581* (FSU, MO). Between Las Margaritas and El Valle de Antón, *Woodson et al. 1234* (GH, MO, NY). COLÓN: Along Río Culebre, above Santa Isabel, *Pittier 4163* (US). DARIÉN: El Río Yape, *Bristan 1421* (MO). Río Chico near Yaviza at junction with Río Chucunaque, *Burch et al. 1104* (GH, MO, US). Bajo Churo, *Davidson 430* (GH). Río Sabanas, 1–3 mi SE of Santa Fé, *Duke 4121* (MO). 1–3 mi SE of Santa Fé on Panamerican Highway, Río Sabana, *Duke 4123* (MO). Between Río Membrillo and Río Subcutí, *Duke 8615* (MO). Río Sambo, 0–5 mi above Río Venado, *Duke 9265* (US). Río Tuira, between Río Punusa and Río Mangle, *Duke 14595* (MO). Along the Sambu River, *Pittier 5531* (F, US). Vicinity of Caná, *Stern et al. 703* (GH, MO, US). Paca below Caná, *Williams 712* (NY). Caná and vicinity, *Williams 962* (NY). LOS SANTOS: Río Tonosí, vicinity of Tonosí, *Lewis et al. 1570* (GH, MO, US). PANAMÁ: 1 km from Altos de Limón, *Aquilera 5* (MO). Arraiján (Alto el Limón), *Atencio 13* (F, MO). La Jaqua, E of Panama City, *Bartlett & Lasser 16377* (MICH). Nueva Emperador, *Carrasco 29* (F, MO). Cerca de Río Tapia, 2 km de la carretera de Tocumen, *Correa & Escobar 1789* (DUKE). Río Majé, ca. 30 minutes by speedboat from Rio Bayano, *Croat 34384* (MO). Along Panamerican Highway just E of Bejuco, *Duke 4552* (GH, MO). Vicinity of El Llano, *Duke 5492* (MO, USF). Between Cañasas and Sabalo, *Duke 14458*

(MO). Pacora, *Dwyer 1223* (MO). Tocumen, *Dwyer 1863* (MO, USF). 2 mi E of Juan Diaz, *Killip 3075* (US). N of Panama City, *Paul 379* (US). Around Alhajuela, *Pittier 2358* (US). Río Tocumen, *Standley 26748* (US). Taboga Island, *Standley 27015* (US). Juan Franco Race Track near Panama, *Standley 27716* (US). Taboga Island, *Standley 27892* (US). Juan Diaz, *Standley 30500* (US). Río Tataré, *Woodson & Schery 998* (MO). Isla Taboga, *Woodson et al. 1497* (GH, MO, NY). SAN BLAS: In flood plain along hills along Río Armilla, ca. 1 km WSW of Puerto Obaldía, *Mori et al. 6832* (MO, USF).

19. SECHIUM

Sechium P. Br., Civ. Nat. Hist. Jam. 355. 1756. TYPE: *S. edule* (Jacq.) Sw.

Chocho Adans., Fam. Pl. 2: 500. 1763. TYPE: not designated.
Chayota Jacq., Sel. Stirp. Amer. *tab. 245*. 1780. TYPE: *C. edulis* Jacq.

Monoecious, tendriled *vines*; stems 5- to 10-sulcate. *Leaves* petiolate, simple, angulate or lobate; tendrils 5-branched. *Staminate flowers* white in axillary, long pedunculate, interrupted racemes; hypanthium hemispheric; calyx 5-lobed; corolla 5-lobed; stamens 3, filaments connate, short, the anthers spreading, 2 anthers bilocular, 1 anther unilocular. *Pistillate flowers* 1 or 2, axillary, the calyx and the corolla as in the staminate flowers, the ovary oblong, 1-carpellate, the ovule solitary, pendulous, the style short, the stigma capitate. *Fruit* green, obovoid, indehiscent, sulcate, echinate or smooth; seed lenticular, large, the testa smooth.

Sechium is a monotypic Neotropical genus.

1. **Sechium edule** (Jacq.) Sw., Fl. Ind. Occ. 1150. 1800.—FIG. 19.

Sicyos edulis Jacq., Enum. Pl. Carib. 32. 1760. TYPE: not known.
Chayota edulis Jacq., Sel. Stirp. Amer. *tab. 245*. 1780. TYPE: not known.
Sechium americanum Poir. in Lam., Encyc. Méth. Bot. 7: 50. 1806. TYPE: not known.
Cucumis acutangulus Descourt., Fl. Méd. Antilles 5: 94. 1827; non L., 1753. TYPE: not known.
Sicyos laciniatus Descourt., Fl. Méd. Antilles 5: 103. 1827, non L., 1753. TYPE: not known.
Sechium cayota Hemsley, Biol. Centr. Amer., Bot. 1: 491. 1880, pro syn.

High-climbing, perennial, monoecious, tendriled *vines*; stems 5- to 10-sulcate, glabrate. *Leaves* broadly ovate to suborbicular, 6–22 cm long, nearly as wide as long, 3- to 5-lobate or angulate, the lobes acute to acuminate, the base deeply cordate, the margin minutely and usually remotely toothed, chartaceous, appearing palmately 5- to 7-veined, the upper surface scabrous with white pustular based trichomes, the upper and the lower surfaces appressed puberulent on the veins; petioles 4–15 cm long, appressed puberulent or glabrate; tendrils 1- to 5-branched, glabrate. *Staminate flowers* in axillary, long pedunculate, interrupted racemes, the rachis 8–30 cm long, puberulent at least in the upper part, the flowers yellow, 2–6 in clusters; pedicels 1–6 mm long, puberulent; calyx hemispheric, the lobes 5–7 mm long, spreading or recurved, glabrate; corolla lobes ovate lanceolate, 12–17 mm long, acute, spreading, obscurely 5-nerved, both the surfaces papillose pubescent; stamens 3, the filaments connate, short, the anthers flexuous, spreading, 2 anthers bilocular, 1 anther unilocular, the connectives with bulbous based cystolythic trichomes; nectiferous disc with 10 pores. *Pistillate flowers* 1–2, often in the same axils as the staminate flowers, the peduncles 1–3 cm long, rapidly elongating in fruit; calyx and corolla as in the staminate flowers;

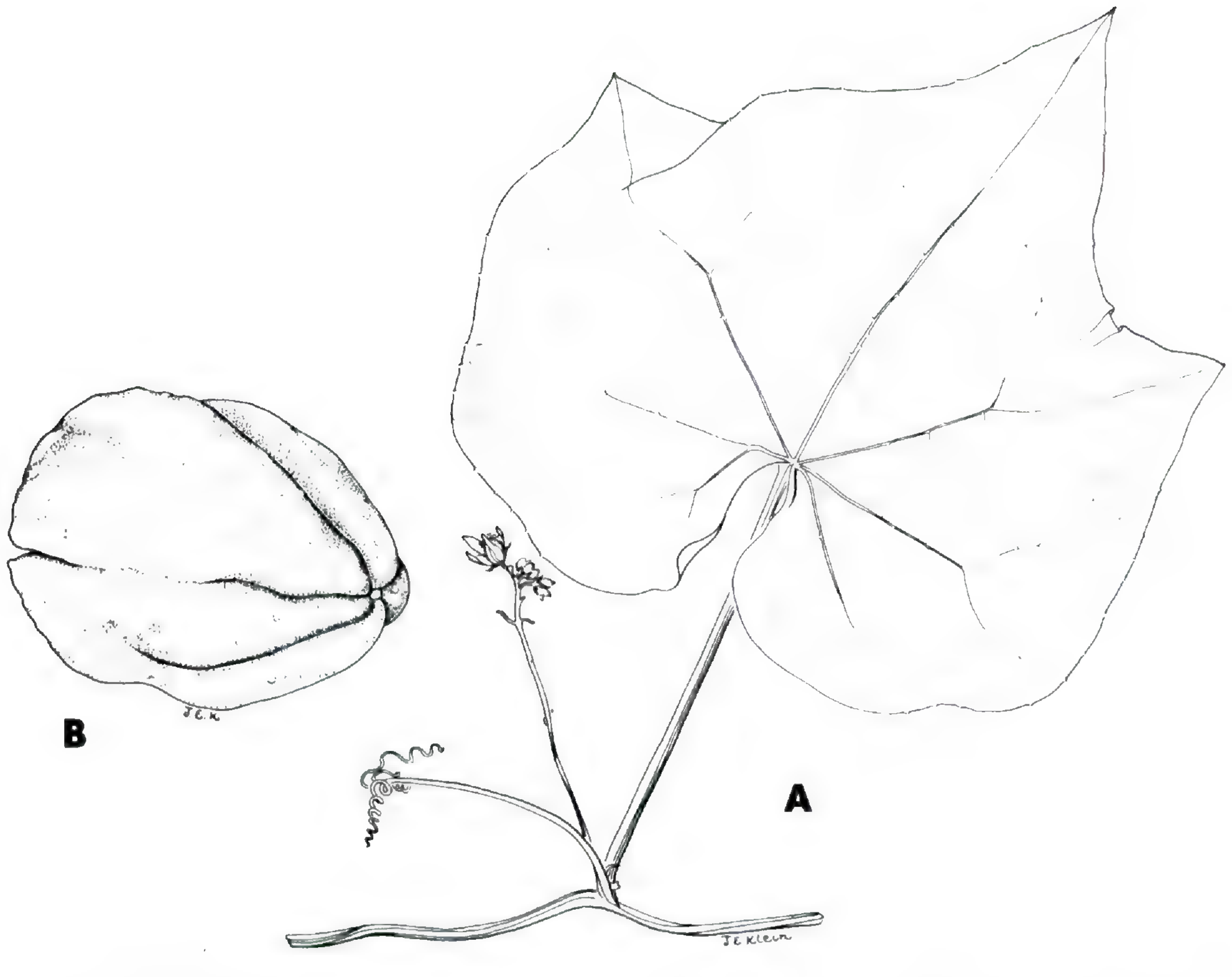

FIGURE 19. *Sechium edule* (Jacq.) Sw.—A. Habit (×½). [After *Ebinger* 957].—B. Fruit (×½). [From photo taken in Panama City market, not vouchered].

ovary oblong, 5-sulcate, pubescent, uniloculate, the ovule solitary, pendulous, the style short, the stigma forming a subglobose, somewhat lobate head; 5–10 nectiferous pouches present. *Fruits* green, obovoid, sulcate, echinate or smooth, 7–20 cm long, firm, indehiscent; seed lenticular, 3–6 cm long, nearly as wide as long, the testa ligneous, smooth.

This species is widely distributed in the Neotropics where it is frequently cultivated for its edible fruits, tubers, and young shoots. Although a native species, it is rarely encountered in the wild.

The fruits are usually boiled and then prepared in a number of ways (e.g. fried, baked, creamed). They can also be made into pickles. The large flat seed is generally cooked and served with the rest of the fruit or is removed for use alone as a table delicacy. The starchy underground tubers are sometimes cooked and eaten. The tender young shoots are occasionally cooked and eaten as spinach.

In Panama and elsewhere the plant is called "chayote." Other names are "quisquil," "guisayote," "huisquil," "huisayote," "chocho," and "christophene" (English). The tubers are sometimes referred to as "raiz" in Costa Rica and "chita" or "chitla" in El Salvador.

CANAL ZONE: U.S. Government Experimental Plantation, Frijoles, *Greenman & Greenman 5155* (MO). Government forest along Las Cruces Trail, *Hunter & Allen 698* (MO). Frijoles, *Standley 31481* (US). CHIRIQUÍ: On mountains above Bambito, 1 mi S of Cerro Punta, *Tyson 5770* (MO). COCLÉ: 2.5 mi above El Valle on road to La Mesa, *Croat 13377* (F, NY, USF). La Mesa, above El Valle de Antón, ca. 2 km W of Cerro Pilón, *Croat 37314* (MO). El Valle de Antón and vicinity, *Duke 13234* (MO); *Ebinger 957* (F, MO, US); *Lewis et al. 2622* (MO); *Seibert 418* (GH, MO, NY).

20. SELYSIA

Selysia Cogn. in DC., Monogr. Phan. 3: 735. 1881. TYPE: not designated.

Monoecious, tendriled *vines*; stems 5- to 10-sulcate. *Leaves* alternate, petiolate, simple, entire or 3-lobate; tendrils simple to 2-branched. *Staminate flowers* solitary or in fascicles, axillary; calyx cup-shaped, 5-lobate; corolla campanulate, deeply 5-lobate; stamens 3, free, inserted on the hypanthium wall, the filaments slender, the anthers suborbicular, variously 1- or 2-locular or all bilocular, the theca apically and basally replicate. *Pistillate flowers* solitary, axillary; calyx and corolla as in the staminate flowers; ovary subglobose, 3-carpellate, 2–6 ovules in each carpel, the ovules erect, the styles 3, connate, the stigmas 3, peltate, 3-lobate. *Fruit* subglobose, indehiscent, baccate, smooth or nearly so; seeds several, compressed, narrowly triangular, apically acute, basally tricornuate, the testa smooth or roughened.

Selysia is a genus of three Neotropical species closely related to *Cayaponia*. The following single species is found in Panama.

1. **Selysia prunifera** (Poepp. & Endlich.) Cogn. in DC., Monogr. Phan. 3: 736. 1881.—FIG. 20.

Melothria prunifera Poepp. & Endlich., Nov. Gen. Sp. Pl. 2: 55. 1838. TYPE: Peru, *Poeppig 2265* (W, not seen).
Selysia aspera Killip ex Jeffrey, Kew Bull. 25: 235. 1971, pro syn.
S. *perlobata* Killip ex Jeffrey, Kew Bull. 25: 235. 1971, pro syn.

Monoecious, tendriled *vines*; stems 5- to 10-sulcate, pubescent to glabrate. *Leaves* simple, the blade broadly ovate to suborbicular in outline, 3-lobate, 10–20 cm long, 9–18 cm wide, the apex acuminate, the base deeply cordate, the margin minutely and remotely denticulate, chartaceous, 3-veined, the upper and the lower surfaces densely to sparsely pubescent on the veins; petiole 3–7 cm long, slender, pubescent to glabrate; tendrils 2-branched. *Staminate flowers* 1–3 in the axils of the leaves; calyx cup-shaped, puberulent, 5-lobate, the lobes linear lanceolate, 2–4 cm long; corolla white, campanulate, ca. 1.5 cm long, the lobes lanceolate, the outer surface puberulent, the inner surface tomentose; stamens 3, the filaments free except where adnate to the hypanthium wall at the base, short, glabrous, the anthers basally and apically replicate, 2 anthers unilocular, 1 anther bilocular. *Pistillate flowers* not seen. *Fruit* red or reddish orange, the pulp white, subglobose or ellipsoid, indehiscent, baccate, 3–4 cm in diameter, the surface lustrous, smooth or nearly so, 3-carpellate, the peduncle 6–14 cm long; seeds 6–19, erect, narrowly triangular, the apex acute, the base 3-cornuate, 12–15 mm long, 6–8 mm wide at the base, compressed, black or brown, slightly roughened.

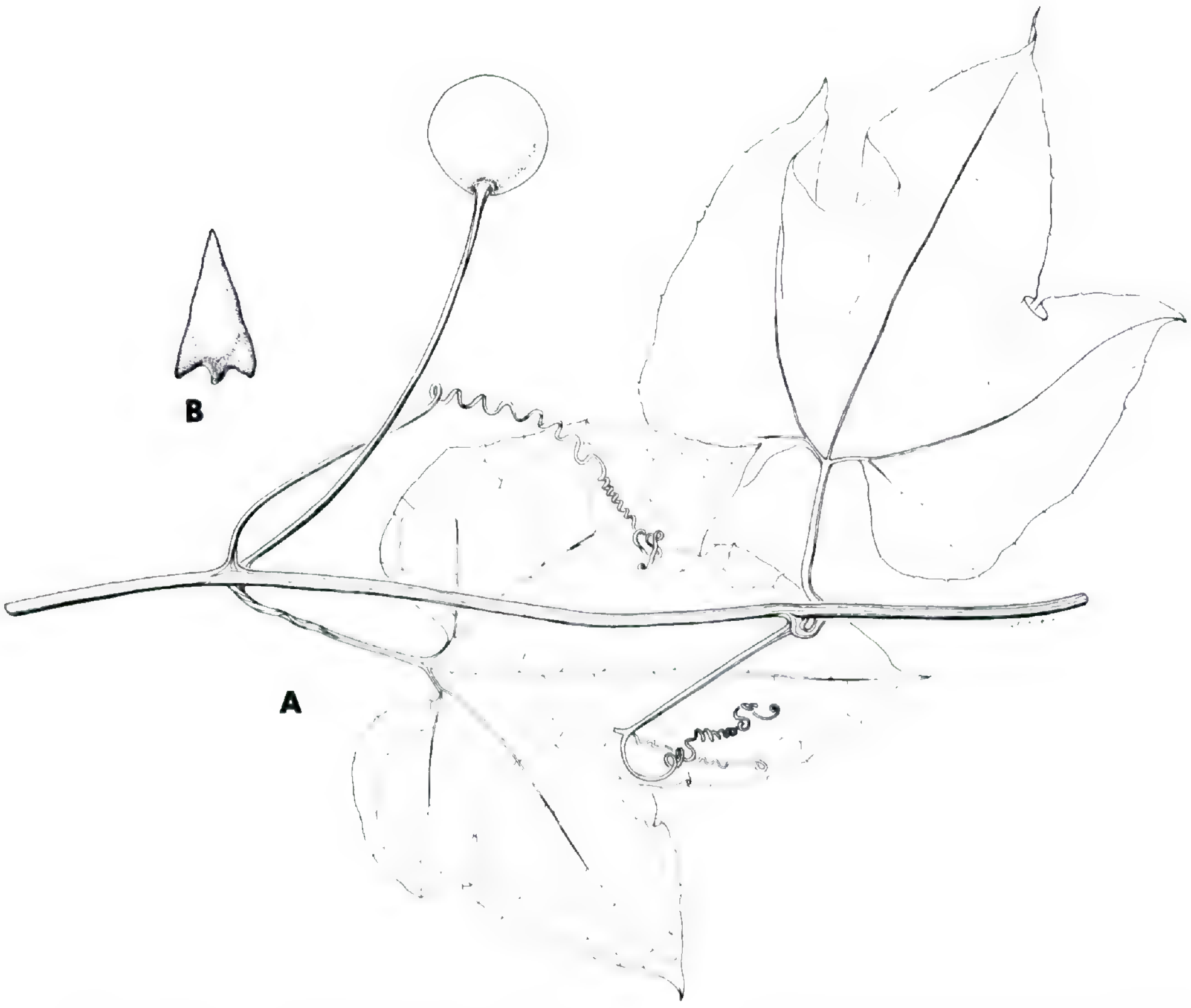

Figure 20. *Selysia prunifera* (Poepp. & Endl.) Cogn.—A. Habit (×⅖). [After *Liesner 593*].—B. Seed (×⅗). [After *Correa & Dressler 270*].

Selysia prunifera is a variable species, ranging from Costa Rica south to Peru and Ecuador. It is uncommon in Panama, occurring in tropical wet forests from sea level up to about 700 m.

BOCAS DEL TORO: Water Valley, Chiriquí Lagoon, *Wedel 1596* (F, GH, MO). CHIRIQUÍ: San Bartolo, 12 km W of Puerto Armuelles, *Busey 527* (MO, NY). COCLÉ: Near La Mesa, *Croat 13362* (MO). La Mesa, above El Valle de Antón, *Weaver & Foster 1631* (DUKE). COLÓN: Carretera a la Zona de Santa Rita, *Correa & Dressler 1827* (MO). Santa Rita Ridge road, 5 mi from highway, *Croat 13181* (MO, USF). Santa Rita Ridge, *Croat 13846* (F, NY). Santa Rita Ridge road 4 mi from Transisthmian Highway to Agua Clara weather station, *Gentry et al. 8856* (MO). Santa Rita Ridge, ca. 5.5–6.0 mi E of Transisthmian Highway, *Lewis et al. 5399* (MO). Santa Rita Ridge Road, *Mori & Kallunki 2781* (MO, USF). DARIÉN: Cocalito, *Dwyer 4699* (MO). PANAMÁ: 11 mi S from Goofy Lake along road to Cerro Jefe, *Correa & Dressler 270* (MO). El Llano-Cartí Road, 7–12 km from Panamerican Highway, *Croat 25109* (MO). Beyond Cerro Jefe, *Duke & Dwyer 15070* (MO). Cerro Jefe, Altos de Pacora, 18.2 km E of Cerro Azul Village (Goofy Lake), *Gentry & Mori 13417* (MO, USF). Campo Tres, 3 mi NE of Altos de Pacora, *Liesner 593* (F, MO, US). Beyond the village of La Eneida, *Luteyn & Foster 1121* (DUKE). 5–10 km NE of Altos de Pacora, *Mori & Kallunki 4986* (MO, USF). El Llano-Cartí Road, 7–12 km from Panamerican Highway, *Mori et al. 4543* (MO, USF). El Llano-Cartí road, 8–12 km N of El Llano, *Nee et al. 8785* (MO). Cerro Campana, summit of upper trail, *Witherspoon & Witherspoon 8469* (MO). SAN BLAS: 2–5 mi S of Mandinga Airport, *Duke 14817* (MO). Mainland opposite Playon Chico, 0–3 mi from Caribbean, *Gentry 6347* (MO).

21. SICANA

Sicana Naud., Ann. Sci. Nat. Bot. sér. 4. 18: 180. 1862. TYPE: S. *odorifera* (Vell.) Naud.

Monoecious, tendriled *vines*; stems 5- to 10-sulcate. *Leaves* alternate, petiolate, lobate; tendrils 3- to 5-branched. *Staminate flowers* solitary, axillary; hypanthium campanulate; calyx 5-lobate, the lobes reflexed; corolla yellow, campanulate, 5-lobate over halfway; stamens 3, the filaments short, slightly connate at the base, the anthers free, the theca sigmoid, flexuous. *Pistillate flowers* solitary, axillary; calyx and corolla as in the staminate flowers; ovary oblong ovoid, 3-carpellate, the ovules numerous, horizontal, the style short, connate, the stigmas 3, obscurely bilobate; staminodes 3. *Fruits* fleshy, cylindric, indehiscent; seeds oblong ovate, compressed, inconspicuously marginate.

Sicana is a monotypic genus native to South America. The single species is cultivated to some extent in Panama and is persistent after cultivation or naturalized in ruderal areas.

1. **Sicana odorifera** (Vell.) Naud., Ann. Sci. Nat. Bot. sér. 4. 18: 181. 1862.—FIG. 21.

Cucurbita odorifera Vell., Fl. Flum. 10. *tab.* 99. 1825. TYPE: not known.
C. euodicarpa Hassk., Hort. Borg. Desc. 1: 305. 1858. TYPE: not known.

Vines; stems puberulent when young, glabrescent. *Leaves* suborbicular, 10–24 cm long, nearly or equally as wide as long, shallowly 3- to 5-lobate, the lobes acute, cordate at the base, chartaceous, the margin undulate denticulate, both the surfaces with white pustular dots, puberulent on the veins, at least near the base; petioles slender, 4–15 cm long. *Staminate flowers* solitary, axillary; hypanthium campanulate, 6–8 mm long, ashy tomentose; calyx lobes 9–12 mm long, broadly lanceolate, ashy tomentose, reflexed; corolla almost fleshy, the lobes ca. 2 cm long, the outer surface tomentose, the inner surface papillate, 5-nerved; stamens glabrous, the filaments 3–5 mm long, ½ as long as the flexuous anthers; peduncle 2–5 cm long. *Pistillate flowers* with the perianth as in the staminate flowers; ovary oblong ovoid, glabrate, 5–6 cm long, the style ca. 1 cm long, the stigma capitate, 8–10 mm wide; staminodes 4–5 mm long. *Fruits* yellow, red, purplish, or dark green, oblong ovoid or cylindric, 30–60 cm long, glabrous, very fragrant; seeds oblong ovate, compressed, marginate, ca. 1 cm long and nearly as wide.

A native of South America, *Sicana odorifera* is cultivated widely in the Neotropics for its fragrant fruits. The fruits, having a pleasant odor, have long been used to scent linens, clothing, etc. or for making preserves. In Panama the plant is called "chila" or "calabaza," "secana," or "olerero."

DARIÉN: Quebrada Tumangati near Santa Fé, *Duke* 8822 (MO). PANAMÁ: Cultivated at Agricultural Experimental Station at Matías Hernández, *Pittier* 6796 (US). 5 mi W of Chepo near Panamerican Highway, *Tyson* 6731 (MO).

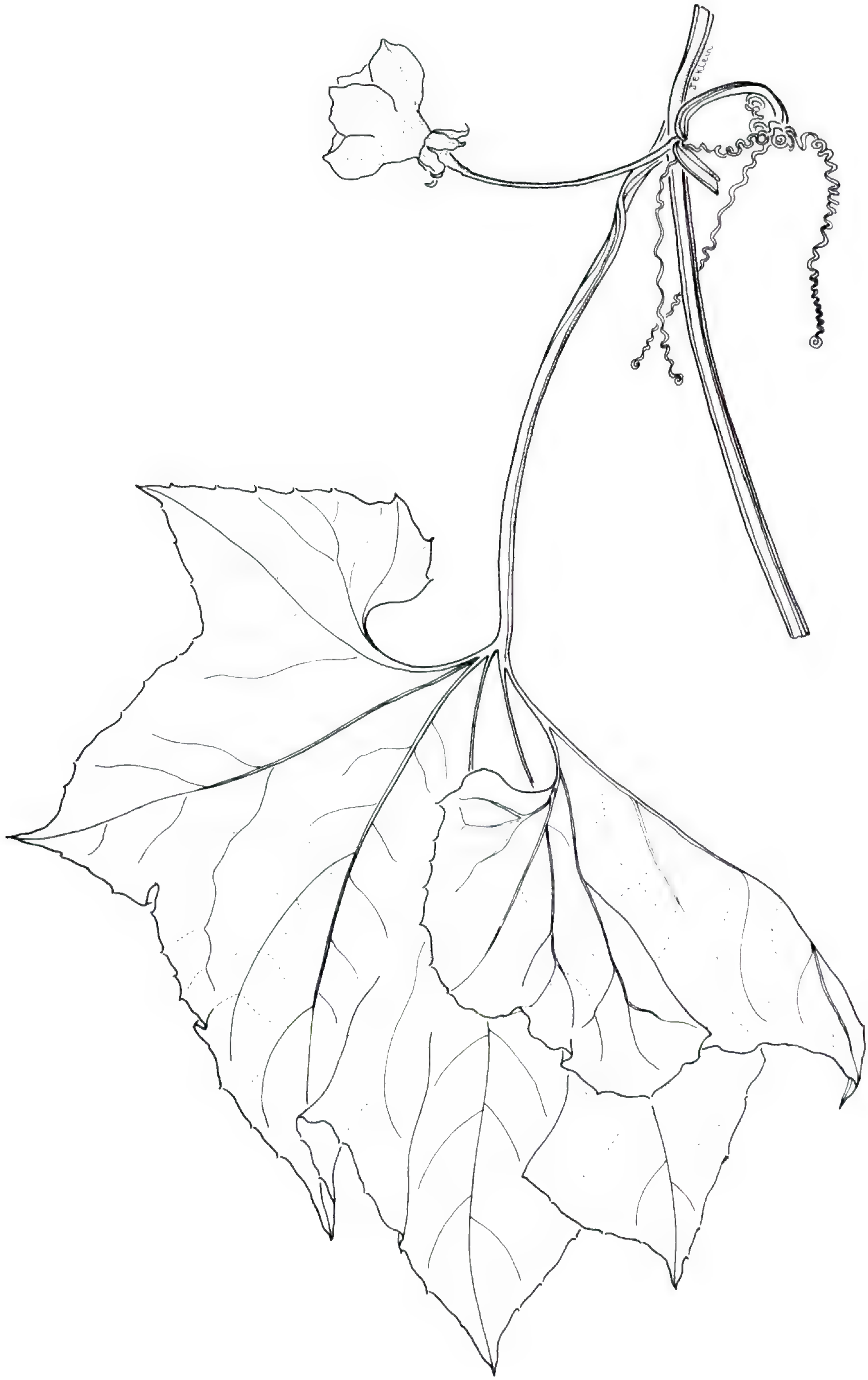

FIGURE 21. *Sicana odorifera* (Vell.) Naud. Habit ($\times 3/10$). [After *Tyson 6731*].

22. SICYDIUM

Sicydium Schlecht., Linnaea 7: 388. 1832; not A. Gray, Boston J. Nat. Hist. 6: 194. 1850. TYPE: S. *schiedeanum* Schlecht.

Triceratia A. Rich. in Sagra, Hist. Cuba 2. 10: 615. 1845. TYPE: *T. bryonioides* A. Rich.

Dioecious, tendriled *vines*; stems 5- to 10-sulcate. *Leaves* alternate, petiolate, cordate; tendrils 2-branched at apex. *Staminate flowers* minute, paniculate, axillary; calyx 5-lobate; corolla rotate, deeply 5-lobate; stamens 3, free, the filaments short, inserted on the hypanthium wall, the anthers straight, 2 anthers bilocular, 1 anther unilocular. *Pistillate flowers* disposed as the staminate flowers; calyx and corolla as in the staminate flowers, the ovary ovoid, uniloculate, the ovule 1, pendulous, the styles 3, linear, spreading, the stigmas linear. *Fruits* globose, fleshy, indehiscent, 1-seeded; seed spherical, emarginate, the testa crustaceous, rugose.

A genus of about six species in the Neotropics with two in Panama.

a. Leaves, stems, and inflorescences densely pubescent; fruits 5–7 mm in diameter; seeds, 4–5 mm in diameter ..... 2. S. *tamnifolium*
aa. Leaves, stems, and inflorescences glabrous or nearly so; fruits 9–12 mm in diameter; seeds, 6–8 mm in diameter ..... 1. S. *coriaceum*

1. **Sicydium coriaceum** Cogn. in DC., Monogr. Phan. 3: 906. 1881. TYPE: Colombia, *Triana 3024* (P, not seen).

Dioecious, tendriled *vines*; stems glandular puberulent to glabrate. *Leaves* ovate, 5.5–12.0 cm long, 3.5–9.0 cm wide, the apex acuminate, the base cordate, the margin entire or slightly undulate, chartaceous or coriaceous, the upper surface minutely pustulate and scabridulous, puberulent on the veins; petals slender, 1–5 cm long; tendrils 2-branched at the apex. *Inflorescences* axillary, paniculate, glandular puberulent to glabrate, many flowered, pedicels capillaceous, to 1 mm long. *Staminate flowers* greenish white, sepals lanceolate, ca. 0.8 mm long, villous on the outer surface; corolla linear lanceolate, ca. 2.5 cm long, spreading, flexuous, the apices slightly incurved, papillose pubescent on both the surfaces, the margin fimbriociliate; stamens short, the anthers quadrate or oblong, the hypanthium disc slightly 5-lobate. *Pistillate flowers* with calyx and corolla as in the staminate flowers; ovary narrowly ovoid, ca. 2 mm long, glandular pubescent; styles capillaceous, apices recurved. *Fruits* black, smooth or nearly so, glandular puberulent or glabrate, 9–12 mm in diameter; pedicels 4–10 mm long; seed brown, deeply verrucose, 6–8 mm in diameter.

This species ranges from Panama to Peru, occurring in tropical moist forests. In Panama it is known only from Barro Colorado Island, but probably occurs elsewhere.

CANAL ZONE: Barro Colorado Island, *Bailey & Bailey 140* (US); *Croat 9572* (F, MO, NY), *12931* (MO).

2. **Sicydium tamnifolium** (H.B.K.) Cogn. in DC., Monogr. Phan. 3: 905. 1881. —FIG. 22.

Fevillea tamnifolis H.B.K., Nov. Gen. Sp. Pl. 7: 175. 1825. TYPE: Colombia, *Humboldt & Bonpland* (P, not seen).

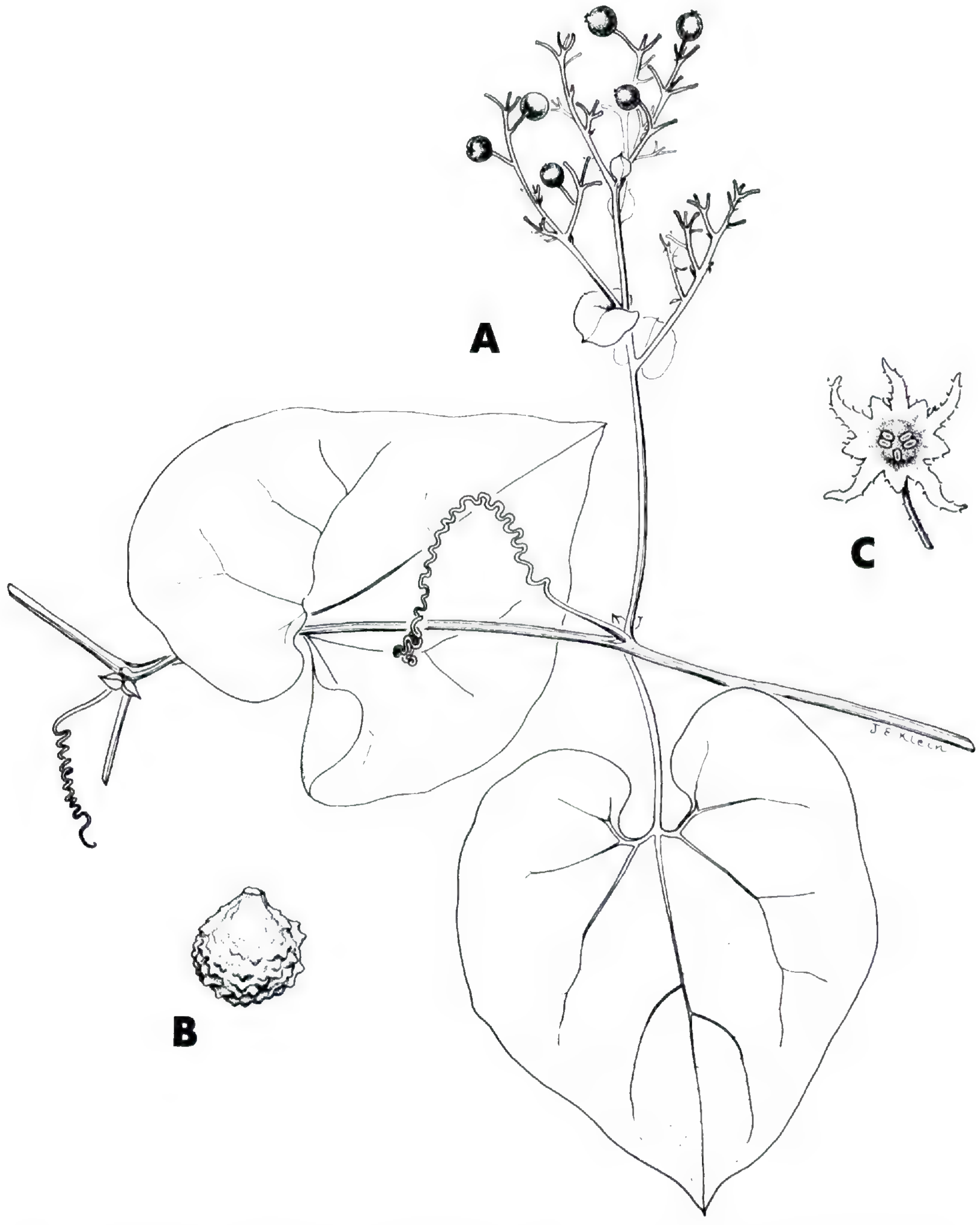

FIGURE 22. *Sicydium tamnifolium* (H.B.K.) Cogn.—A. Habit (×⅗).—B. Seed (×3⅗). [After *Stern et al. 303*].—C. Flower (×6). [After *Duke* 5385].

Triceratia bryonioides A. Rich. in Sagra, Hist. Cuba 2. 10: 615. 1845. TYPE: not known.
Sicydium tamnifolium var. *dussii* Cogn., Bull. Soc. Roy. Bot. Belgique 30(1): 277. 1891. TYPE: Costa Rica, *Duss* 93 (BR, not seen).

Dioecious, tendriled *vines*; stems densely pubescent, at least when young, rarely glabrate. *Leaves* ovate, 7–10 cm long, 5–8 cm wide, the apex acute or acuminate, the base cordate, the margin entire, membranaceous to subcharta-

ceous, the upper surface minutely white pustulate, slightly scabrous, both the surfaces pubescent at least on the veins; petioles slender, 2–5 cm long, densely pubescent to glabrate; tendrils slender, 2-branched at the apex. *Inflorescences* axillary, paniculate, usually densely so, trichomes glandular tipped and eglandular, many flowered; pedicels capillaceous, to 1 mm long. *Staminate flowers* greenish white; sepals triangular, ca. 0.5 mm long, villous on the outer surface; corolla linear lanceolate, ca. 1.5 mm long, spreading, the apex slightly incurved, papillose pubescent on both the surfaces, the margin fimbriociliate; stamens short; anthers quadrate or oblong, the hypanthium disc slightly 5-lobate. *Pistillate flowers* with the calyx and the corolla as in the staminate flowers; ovary ovoid, ca. 1.5 mm in diameter, pubescent with glandular and eglandular trichomes, the style capillaceous, divergent at the apex. *Fruits* black, smooth, puberulent or glabrate, 5–7 mm in diameter; pedicel 4–10 mm long; seed brown, deeply verrucose, ca. 4–5 mm in diameter.

Sicydium tamnifolium ranges from Mexico to Peru and into the Caribbean, occurring in thickets and open forests at low elevations. It is of fairly frequent occurrence in Panama.

BOCAS DEL TORO: Changuinola Valley, *Dunlap 571* (US). Without definite locality, *Wedel 468* (F, MO). Water Valley, Chiriquí Lagoon, *Wedel 1815* (F, GH, MO). Old Bank Island, Chiriquí Lagoon, *Wedel 2144* (MO). CANAL ZONE: Near beach at Ft. Kobbe, *Duke 4214* (MO), *4710* (GH, MO). Bridge near entrance to Boy Scout Camp, *Dwyer 7484* (MO). Madden Dam, Boy Scout Camp Road, *Dwyer & Elias 7484* (GH, MO). Road between Transisthmian Highway and Madden Dam, *Gentry 6742* (GH, MO). Around Gamboa, *Pittier 4819* (GH, US). Sousa Hill, Balboa, *Standley 26261* (US). Balboa, *Standley 25610* (US). Las Cascadas Plantation near Summit, *Standley 25774* (US). Balboa, *Standley 27174, 29250* (both US). Las Cascadas Plantation near Summit, *Standley 29522* (US). Juan Diaz, *Standley 30474* (US). Río Cocolí, Road K-9, *Stern et al. 303* (GH, MO, US). Fort Clayton, Cardenas Creek area, *Tyson 1276* (DUKE, MO). 2 mi N of Cocolí, *Tyson 1641* (DUKE, MO). Curundú, near Survival School, *Tyson 4182* (MO). Gamboa, *Tyson et al. 4580* (MO). CHIRIQUÍ: Río Chorcha, *Gentry 4857* (MO, NY). Quebrada Melliza, 6 mi S of Puerto Armuelles, *Liesner 489* (MO, US). DARIÉN: Along Río Pirre, *Duke 4969* (GH, MO, US). Across Río Chucunaque from Pinogana, *Duke 5176* (GH, MO). Panamerican Highway near Boca del Cupa, *Duke 5385* (MO). Isla Boca Grande, *Duke 8840* (MO, US). Río Sabana, Santa Fé, *Leopold 240* (MO). Along the Sambú River, *Pittier 5564* (US). Vicinity of El Real, Río Tuira, 1 mi from Pinogana near Quebrada Chuito, *Stern et al. 108* (GH, MO, US). PANAMÁ: Pacora, *Dwyer 1228* (MO). Sabanas, near Chepo, *Hunter & Allen 90* (MO). Taboga Island, *Maxon 6915* (US); *Pittier 3549* (US); *Standley 27085, 27097* (both US). Between Matías Hernández and Juan Dias, *Standley 32003* (US). Isla Taboga, *Woodson et al. 1464* (AA, F, MO, NY). SAN BLAS: Around Puerto Obaldía, *Pittier 4379* (US).

23. SICYOS

Sicyos L., Sp. Pl. 1013. 1753; Gen. Pl. ed. 5. 1754. TYPE: *S. angulata* L.

Sicyoides P. Miller, Gard. Dict. abr. ed. 4. 1754. TYPE: not designated.
Baderoa Bertol. ex Hook., Misc. Bot. 3: 324 1833. TYPE: *B. bryoniaefolia* Bertol.

Monoecious, tendriled *vines*; stems 5- to 10-angled or -sulcate. *Leaves*, petiolate or the uppermost sessile, subentire or deeply lobate; tendrils 3- to 5-branched. *Staminate flowers* in racemes, panicles or umbelloid clusters, inflorescences long pedunculate; calyx shallowly and broadly campanulate to rotate,

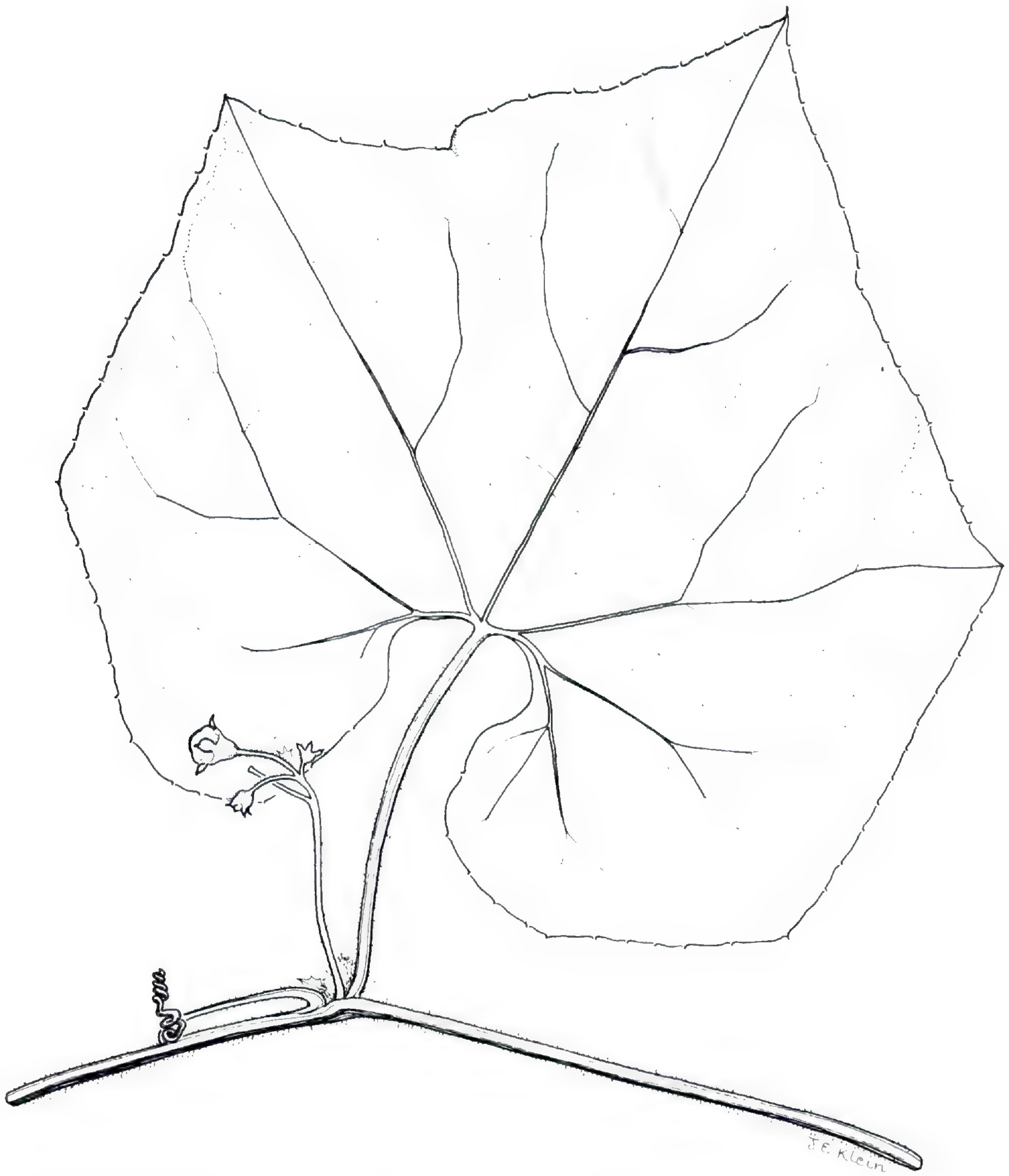

FIGURE 23. *Sicyos polyacanthus* Cogn. Habit (×⅗). [After *Skutch* 3965—Costa Rica].

5-toothed; corolla salverform, the limb 5-lobate, spreading; stamens 3 (rarely 2 or 5), the filaments connate; anthers connate or free, the theca flexuous to nearly straight. *Pistillate flowers* in sessile clusters or in short pedunculate umbelloid heads, borne in the same axils as the staminate flowers; ovary ovoid to fusiform, setose or aculeate, rarely unarmed, 1-celled, the ovule solitary, pendulous, the style subequalling the corolla tube, the stigma broad, 2- to 3-lobate. *Fruits* dry, ovoid, echinate, spiny, or rarely unarmed; seeds conforming to the locule, the testa reticulate or pitted.

Sicyos is a genus of about 25 species, all of the New World, mostly tropical and subtropical, although a few species are temperate. The following single species was reported from Panama by Cogniaux (1881), but no specimens have been examined. It is, however, to be expected.

1. **Sicyos polyacanthus** Cogn. in Mart., Fl. Bras. 6(4): 107. 1878. TYPE: Brasil, *Gardner 3744* (B, isotype, probably destroyed, not seen; photo, MO).—FIG. 23.

High-climbing *vines*; stems slender, scabrous or villous. *Leaves* cordate to suborbicular, 8–25 cm long, nearly as wide as long, shallowly 3- to 5-lobate, the apex of the lobes acute, the base deeply cordate, the margin undulate dentate, submembranaceous, the upper surface pustulate dotted, scabrous, pubescent on the veins, at least near the base, the lower surface villous pubescent on the veins; petioles 8–20 cm long, slender, pubescent, or villous, distinctly striate; tendrils 2- to 5-branched. *Staminate flowers* axillary, racemose, the rachis 10–30 cm long, sulcate, pubescent, villous, or glabrate, flowered in the upper part; calyx broadly campanulate, the lobes linear to triangulate, 2–3 mm long, sparsely villous; corolla yellowish green, the lobes spreading, triangular lanceolate, 5–7 nerved, 3–4 mm long, slightly glandular papillose on both the surfaces; stamens 3, connate, the anthers connate, capitate, the theca flexuous. *Pistillate flowers* in capitate clusters at the end of the peduncle; peduncle short; calyx and corolla as in the staminate flowers; stigma broad, 3- to 5-lobed, the ovary elliptic, setose. *Fruits* ovoid, compressed, ca. 1 cm long, 5–6 mm wide, the seta 2–3 mm long; seed ovoid, 4–6 mm long.

In addition to this species, *Sicyos parviflorus* Willd. ranges from Mexico to South America and is to be expected in Panama. It is distinguished from *S. polyacanthus* by its unarmed fruits.

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ERRATA

Floristic Inventory of the Tropics: A Correction

In a recent publication in this journal (Prance, 1978) entitled "Floristic Inventory of the Tropics: Where do we Stand?", the figures in one table were incorrect by two decimal places. This alters the comparison between Malesia and other parts of the tropics and so a corrected comment is supplied here.

In Table 3 of Prance (1978) the figures given for density index of herbarium collections per unit area were incorrect. These figures were taken from *Flora Malesiana*, Ser. 1, 8 (1): 3. 1974, where it was not made clear that the density index was calculated for the number of collections per 100 km^2 rather than per km^2. Reference to the footnote of the original density indices published in *Flora Malesiana*, Ser. 1, 1: cviii–cxii. 1950 shows that density index was calculated as specimens per 100 km^2.

In Prance (1978) the only other area for which a comparable density index was prepared was Central America, a region for which it was possible to obtain good estimates of the number of collections made in each country. Table 1 is a new comparison of the Malesian density indices with those of Central America using collections per 100 km^2 in all cases. It can be seen from this table that, interestingly, there is not a large difference in the level of collecting between Malesia and Central America. With the exception of Nicaragua, Central America is slightly better collected. Some areas of Malesia are better collected than any in Central America, but the average density index for Central America is higher than that of Malesia.

TABLE 1. Collecting density index of herbarium collections per 100 km^2 in Malesia and Central America.

Region	Density Index 1950	Density Index 1972	Density Index 1977
1. Sumatra	18	21	
2. Malay Peninsula	145	175	
3. Java	187	197	
4. Lesser Sunda Is.	25	36	
5. Borneo	12	26	
6. Philippine Is.	62	69	
7. Celebes	18	19	
8. Moluccas	43	48	
9. New Guinea	12	26	
10. Guatemala			73
11. Belize			112
12. El Salvador			37
13. Honduras			36
14. Nicaragua			3.8
15. Costa Rica			138
16. Panama			132
	$\bar{x} = 33$	$\bar{x} = 44$	$\bar{x} = 62.96$

In Figure 1 on page 696 of the same issue, the number of species confined east or west of the Suai-Sibuti drainage should read 13 rather than 3.

South America, however, remains much less collected than either Central America or Malesia, and all other comparisons made in the original paper remain correct. This correction does not alter the fact that further collecting is needed in both Central America and Malesia before the primary habitats are completely destroyed.

Literature Cited

Prance, G. T. 1978. Floristic inventory of the tropics: Where do we stand? Ann. Missouri Bot. Gard. 64: 659–684.

I thank Dr. Marshall Crosby for examining the statistics carefully and pointing out to me the error in density index discussed above.

—*Ghillean T. Prance, The New York Botanical Garden, Bronx, New York 10458.*

PREPARATION OF MANUSCRIPT

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St. Louis, Missouri 63110.

For subscription information contact the Business Office of the Annals,
P.O. Box 368, 1041 New Hampshire, Lawrence, Kansas 66044.

Subscription price is $45 per volume U.S., Canada, and Mexico,
$50 all other countries. Four issues per volume.

Second class postage paid at Lawrence, Kansas 66044

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ANNALS
OF THE
MISSOURI BOTANICAL GARDEN

VOLUME 65 1978 NUMBER 2

SYSTEMATIC STUDIES IN AFRICA: THE TWENTY-FOURTH SYSTEMATICS SYMPOSIUM

MARSHALL R. CROSBY[1]

The Twenty-fourth Systematics Symposium at the Missouri Botanical Garden, held 14–15 October 1977, was devoted to an analysis of the biota of Africa. This topic was chosen because within the past few years the Garden has unquestionably become the North American center for the study of the African flora and an in-depth review of this important continent would be informative to North American biologists and perhaps stimulate further investigations by them.

The Garden's herbarium now contains an estimated 300,000 specimens from Africa. The nucleus of the collection was among the J. J. Bernhardi herbarium, purchased for the Garden by George Engelmann in Germany in 1859. The Bernhardi collection contained a total of about 60,000 specimens and among these were African collections made by Drége, Eklon, and Zeyher (D'Arcy, 1971). Acquisition of African material was passive until the curatorship of the herbarium by R. E. Woodson from 1948–1963, who especially undertook a program of photographing African type specimens in Kew and the British Museum (Natural History). During this period the total herbarium grew in size from about 1.3 million specimens to about 1.6 million.

Gillett (1968), noting the aid being provided by North America to Africa and the "supply of plant commercial products from Africa to North America," called for the establishment of "an institution in North America where African plants are studied." Specifically Gillett pointed out that American students and professionals visiting Africa should have access to African plants deposited in North America for use in their work. And, conversely, Africans working in North America should have ready access to African plants. Generally, a significant African collection in North America would contribute to the overall development of plant systematics and duplicate collections should be "distributed about the world and not restricted . . . to Europe," Gillett also stated.

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ANN. MISSOURI BOT. GARD. 65: 367–368. 1978.
0026-6493/78/0367–0368/$00.25/0

In response to Gillett's call, W. H. Lewis, who headed the Garden's herbarium from 1964 through 1971, polled curators of other major North American herbaria concerning the idea of having the Missouri Botanical Garden the "repository of African material in North America" (Lewis, 1970). The replies encouraged the Garden to assume this role, and with the cooperation and support of individuals and institutions, an active program acquiring African specimens, mainly through exchanges and purchases, was begun. Annual receipts grew from about 500 in 1965 to over 5,300 in 1968. During Lewis's tenure, the herbarium grew from about 1.6 million to 2.0 million specimens.

With the 1975 appointment of Peter Goldblatt as the first B. A. Krukoff Curator of African Botany, the Garden's African program moved from one of simple acquisition of plants to one of active research and exploration. Goldblatt has initiated an ongoing program of research on the Iridaceae of southern Africa, and he and other staff members made ten collecting trips to Africa and Madagascar from 1972 through 1977. The collection of African material continues to grow, with over 23,000 specimens received in 1977. At the end of 1977 the total collection numbered slightly over 2.5 million.

The Twenty-fourth Symposium received partial financial support from National Science Foundation grant DEB-7504046 to the Missouri Botanical Garden. The award of this grant made possible the appearance at the Symposium of J.-F. Leroy, Paris, J. Quézel, Marseilles, and J. P. M. Brenan, Kew, whose contributions follow, together with that of Peter Goldblatt, in this issue of the *Annals*. Other papers presented were: C. D. Michener, "The Biogeography of Bees with Special Reference to Africa"; H. B. S. Cooke, "African Mammals and the Fossil Record"; and, the evening address, C. Howell, "Plio/Pleistocene Hominids and Their Paleoenvironmental Settings in Africa." The latter three papers will be published in a forthcoming issue of the *Annals of the Missouri Botanical Garden.*

LITERATURE CITED

D'ARCY, W. G. 1971. Mysteries and treasures in Bernhardi's herbarium. Missouri Bot. Gard. Bull. 69(1): 20–25.

GILLETT, J. B. 1968. A North American institute for the study of the African flora needed. Taxon 17: 106–107.

LEWIS, W. H. 1970. Missouri Botanical Garden as repository of African material in North America. Taxon 19: 345–346.

This entire Symposium, Vol. 65, no. 2, pp. 367–589 will be available in late February 1979 as a reprint entitled "Phytogeography of Africa." This softbound publication will cost $6.00 per copy (if invoice is needed, a $1.00 fee will be added). Send orders to AFRICA, Garden Gate Shop, Missouri Botanical Garden, 2345 Tower Grove Ave., St. Louis, Missouri 63110, U.S.A.

AN ANALYSIS OF THE FLORA OF SOUTHERN AFRICA: ITS CHARACTERISTICS, RELATIONSHIPS, AND ORIGINS[1,2]

PETER GOLDBLATT[3]

ABSTRACT

Southern Africa, including Namibia (South West Africa), South Africa, Lesotho, Swaziland, and Botswana, covers an area of ca. 2.5 million km². The flora comprises ca. 18,500 species in 1,930 genera. There are 10 endemic families, while 80% of the species and 29% of the genera are endemic. Of the five phytogeographic regions recognized, the Cape Floristic Region is the richest and most distinctive, and in this small area there are some 8,550 species in 957 genera. Most of the subcontinent is arid to semiarid. Its rich and diverse flora, contrasting with the relatively depauperate tropical African flora, is believed to have evolved gradually since the early to mid-Tertiary at the southern edge of the tropics as Africa became progressively drier, partly from an ancient southern African temperate flora and partly from a tropical African forest flora. The large number of species in the Cape Region and adjacent arid areas probably evolved recently in the last 1–2 million years as the climate fluctuated violently during the Pleistocene. Peculiarities of the flora include an unusually high proportion of petaloid monocots, a wealth of succulents, mainly in winter rainfall arid areas, large numbers of sclerophyllous to microphyllous shrubs, and very few annuals.

The first major collections of plants from southern Africa began to arrive in Europe in the late seventeenth and early eighteenth century at the time when Linnaeus was formulating his principles of plant classification and nomenclature. These first examples caused great excitement in the scientific community, for many of them were remarkably different from anything known at the time: the first Proteaceae, Restionaceae, Cunoniaceae, and Bruniaceae, to mention a few families, as well great numbers of succulents and geophytic plants which were then and still are greatly sought after in the horticultural world.

Such was the interest stimulated by these plants that southern Africa was one of the first areas outside the European sphere to be explored botanically, Linnaeus's most famous pupil Thunberg being sent there in 1765 for several years. Little did the botanists of northern Europe realize that the source of these amazing plants was entirely unrepresentative of the African flora as a whole. In fact, almost all the early plants were collected in or near the Dutch settlement of Cape Town at the southwestern tip of the continent. It was not until the early nineteenth century that exploring naturalists moving north across the semidesert Karoo, and eastwards, encountered the rolling savanna plains, with both the plants and animals we now associate with Africa generally.

The area where these first southern African plants were found is now known botanically as the Cape Floristic Region, often regarded as one of only six

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[1] I wish to thank all those listed personally on page 373 who helped with this project, providing accurate data for particular groups. I also thank Peter Raven for his extensive and critical review of the manuscript, and O. M. Hilliard and D. I. Axelrod for their many helpful comments. I must also acknowledge with gratitude my wife Margaret for her assistance in assembling data and in preparing the manuscript.

[2] Supported in part by grant DEB 76-19907 from the U.S. National Science Foundation.

[3] B. A. Krukoff Curator of African Botany, Missouri Botanical Garden, 2345 Tower Grove Avenue, St. Louis, Missouri 63110.

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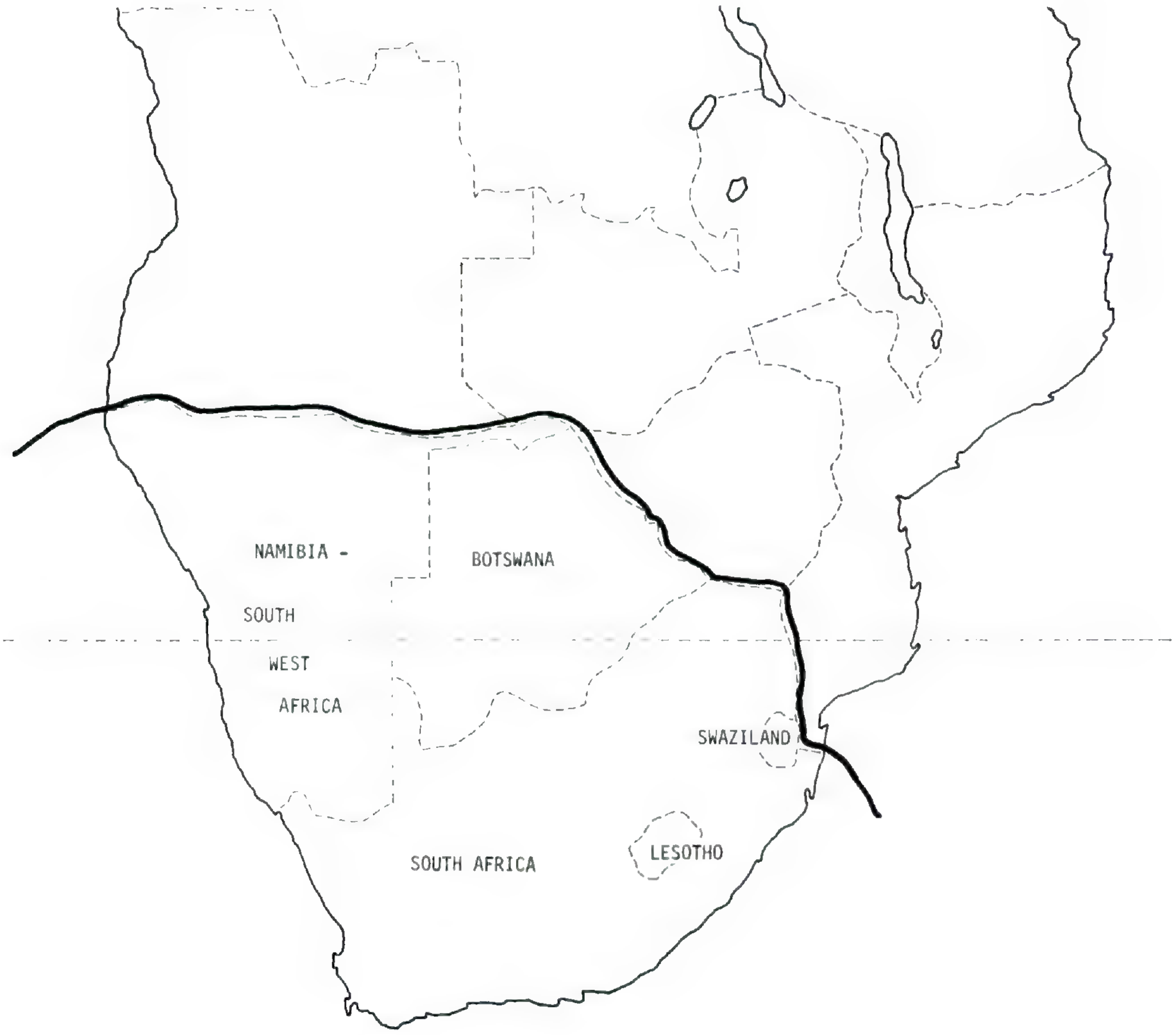

Figure 1. Southern Africa as treated in this paper includes the entire area below the heavy line, with the countries South Africa, Botswana, Lesotho, Swaziland, and Namibia (South West Africa).

Floral Kingdoms in the world (Good, 1974; Takhtajan, 1969). Though small in area, less than 4% of the total land surface of southern Africa as treated here, the flora of this region has come to exemplify in most minds that of southern Africa. The Cape Floristic Region, with its many remarkable and unique characteristics, is analyzed in particular detail in the following pages, with less attention being devoted to the other floristic regions of southern Africa.

Geographical Limits

Southern Africa in this analysis includes the countries of South Africa, Lesotho, Swaziland, Namibia (South West Africa), and Botswana to the north (Fig. 1). This encompasses an area of some 2.5 million km^2, complementing Brenan's delimitation of tropical Africa (this symposium). Ideally we wished to define tropical and southern Africa in phytogeographic or climatic terms, but almost all of the available botanical data are based on political boundaries, and we have found it practical to accept this situation. Perhaps a third of this total

TABLE 1. Comparison of native genera and species of vascular plants of various regions.

Region	Area $10^3 \times km^2$	Genera	Endemic Genera	Species	Endemic Species
Southern Africa	2,573	1,930	560(29.0%)	18,532	14,850(80.3%)
Cape Floristic Region	89	957	198(20.7%)	8,550	6,252(73.1%)
Cape Peninsula[a]	0.47	533	1 (0.2%)	2,256	157 (7.0%)
Natal[b]	91	1,238	?	4,826	?
Namibia[c]	827	910	22 (2.4%)	3,210	?
Australia[d]	7,716	?	?	15,000[g]	85%
Gray's Manual Area[a] (Eastern North America)	3,238	849	6 (0.%7)	4,425	599(13.5%)
Europe[e] (*Flora Europaea*)	10,000	1,340	?	10,500	3,500 (33%)
California Floristic Province[a]	324	795	50 (6.3%)	4,452	2,125(47.7%)
British Isles[a]	308	545	0 (0%)	1,443	17 (1.2%)
New Zealand[a]	268	393	39 (9.9%)	1,996	1,618(81.1%)
Hawaii[a]	16.6	253	31(12.3%)	1,897	1,751(92.3%)
Carolinas[a]	217	819	1 (0.1%)	2,995	23 (0.8%)
Sonoran Desert[a]	310	746	20 (2.7%)	2,441	650(26.6%)
Guatemala[a]	109	1,799	?	7,817	?
West Tropical Africa[f]	4,500	1,742	?	7,500	(ca. 37%)

[a] Data from Raven & Axelrod (1978) who give additional comparative information.
[b] Ross (1973), including introduced species.
[c] Merxmüller (1971 and pers. comm.); data on endemic genera are added by myself.
[d] Specht et al. (1974).
[e] Webb (1978), based on estimates of native genera and species.
[f] Data from Hepper (1971).
[g] Ride (1978) estimates ca. 25,000 species for Australia.

area, including a considerable portion of Namibia and Botswana, as well as a small segment of the South African province of the Transvaal, lies north of the tropic of Capricorn. Nevertheless, as the following pages will show, southern Africa, though floristically heterogeneous, shares few species with tropical Africa and does form a convenient geographic unit so that it can be considered the south temperate element of the African flora.

NUMBERS OF GENERA AND SPECIES

The native flora of southern Africa, including Pteridophytes and Gymnosperms, comprises some 226 families and 1,930 genera with 18,532 species (Table 1). Endemism is relatively high, with 10 families, including the gymnosperm Stangeriaceae and the dicotyledonous Achariaceae, Greyiaceae, Bruniaceae, Penaeaceae, Stilbaceae, Grubbiaceae, Roridulaceae, Retziaceae, and Geissolomataceae (Table 3). The latter six are exclusive to the Cape Region, the Bruniaceae predominantly so, and the three remaining are centered to the east also in mesic conditions.

Of the 1,930 genera, 559 or 29% are endemic and no less than 14,850 or 80.3% of 18,532 species are endemic. These figures indicate even more strongly than the lines limiting phytogeographic zones (Fig. 2) that the southern African flora is remarkably distinct. Much of the richness lies in the Cape Region where there are 8,550 species of which 73%, or 6,252 species, are endemic. This area includes only ca. 89,000 km^2, or less than 4% of the total region under consideration. Excluding the Cape Floristic Region, southern Africa is thus floristically

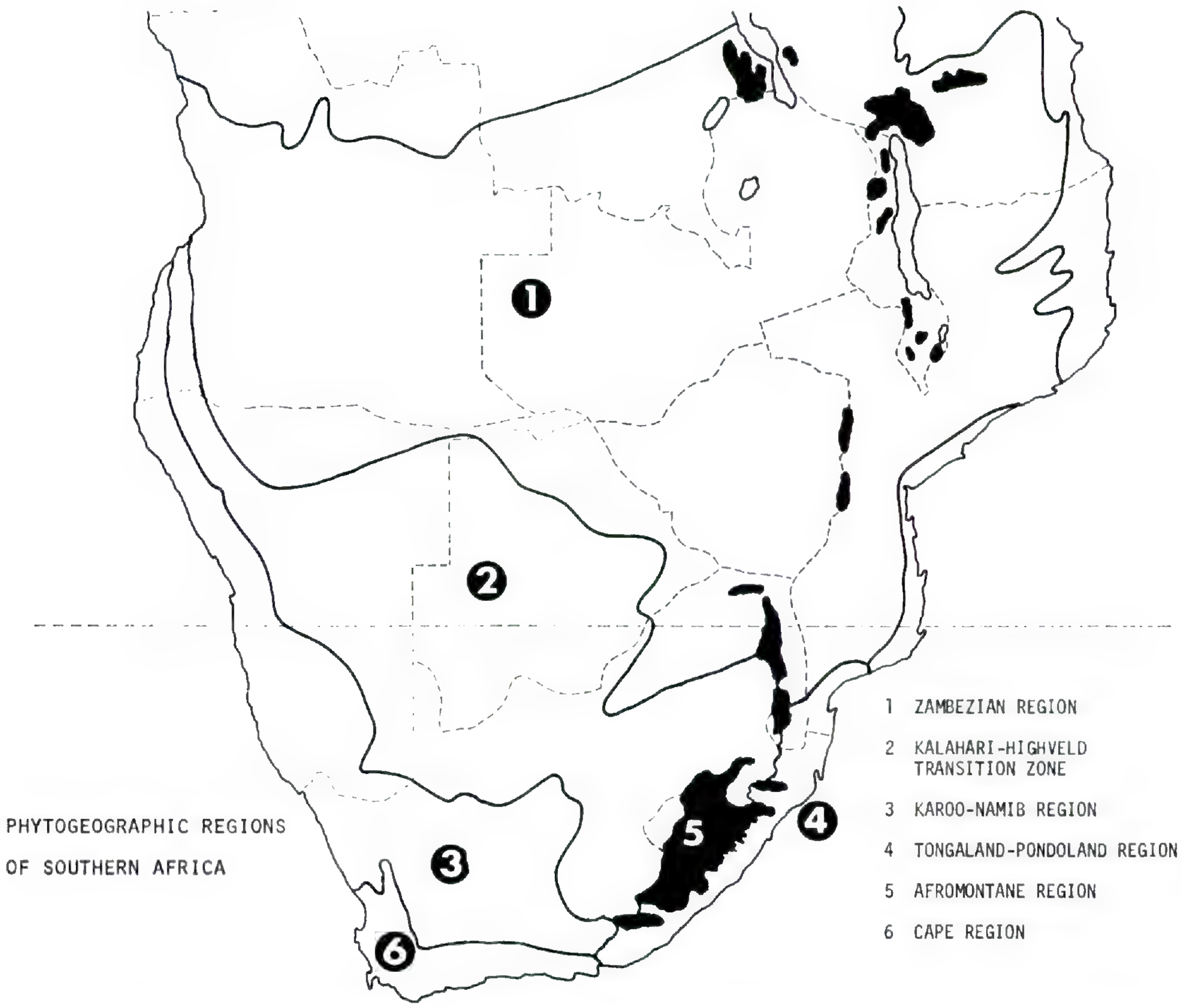

Figure 2. Phytogeographic regions of southern Africa following White (1976a, 1976b, 1978), with some changes to the Cape Region.

much poorer although in area barely reduced. Southern Africa, even excluding the Cape, is still rich with some 1,732 genera and 12,280 species occurring outside the Cape Region. This figure is clearly high when compared with that characteristic of the adjacent tropical *Flora Zambeziaca* area (Zambia, Malawi, Mozambique, Rhodesia, and Botswana) of some 2.6 million km^2, with an estimated 6,000 species (Exell, 1971). It even exceeds the total for Zaïre, Burundi, and Rwanda, an area with about 10,000 species and an estimated 33% endemism in 2.3 million km^2 (Brenan, this symposium) in a region with a rich tropical flora, and it is far richer than west tropical Africa (Hepper, 1971) which has an estimated 7,500 species in 4.5 million km^2.

References and Sources

Prime sources of the data treated here are firstly *Flora Capensis* (Harvey & Sonder, 1859–1865; Thiselton-Dyer, 1896–1933) produced over the years 1860–1925, a flora treating all temperate South Africa which included some 11,705 species. The flora is now being replaced by the *Flora of Southern Africa* (Codd et al., 1963–), the first volume of which appeared in 1963, but as only a few

families have been treated, *Flora Capensis* and the numerous generic monographs and revisions subsequently published have provided most information. There are in addition five modern regional floras for southern Africa, *Prodromus Einer Flora von Südwestafrika* (Merxmüller, 1966–1972) for Namibia, *The Flora of Natal* (Ross, 1972), *Flora of Lesotho* (Jacot-Guillarmod, 1971), *The Flora of Swaziland* (Compton, 1976) and *Flora of the Cape Peninsula* (Adamson & Salter, 1950).

Most problems were encountered in dealing adequately with families or genera not revised since their treatment in one of the early volumes of *Flora Capensis*, as subsequent changes have often been extensive and the early volumes give little distributional data. In many cases I have had to refer to herbarium collections, mainly in South Africa, and to consult authorities for some groups. In particular the following provided the most up to date information, often not yet in print (which will explain certain conflicts with published data): J. P. Rourke (Proteaceae, Stilbaceae); I. Williams (Rutaceae—Diosmeae); E. Esterhuysen (Restionaceae—some 45 undescribed species are taken into account); E. A. Schelpe (Orchidaceae and Pteridophytes); E. G. Oliver (Ericaceae); B. Bayer (*Gasteria*, *Haworthia*, succulent Asclepidaceae); H. Glen (Mesembryanthemoideae in general, especially *Lampranthus*, *Disphyma*, *Gibbaeum*); L. E. Codd (Labiatae); A. A. (Mauve) Obermeyer (*Ornithogalum*, Juncaceae); H. Tölken (Crassulaceae); R. M. Polhill (Papilionoideae in general, *Crotalaria*); M. Thompson (Hypoxidaceae); B. Nordenstam (Compositae generally, *Helipterum*, *Othonna*, Senecioneae, also Liliaceae—*Wurmbea*, *Ornithoglossum*); A. J. M. Leeuwenberg (Loganiaceae); D. Wiens (Loranthaceae); O. Leistner (Malvaceae); A. Rommel (*Amellus*); L. Leach (Asclepiadaceae—Stapelieae, succulent Euphorbias); T. Norlindh (Arctoteae and *Garuleum*); H. E. Wanntorp (*Microloma*); O. M. Hilliard (*Helichrysum*, Drakensberg Flora); H. Rasmussen (*Knowltonia*). Data for Iridaceae were compiled by myself and also include unpublished information.

The families recognized for this work (Appendix 1) are those currently accepted by the Kew Herbarium with minor exceptions. *Retzia* is not included in Solanaceae, but placed in its own family (Dahlgren, 1975; Goldblatt & Keating, 1976) while *Dracaena* remains in Liliaceae and *Heteropyxis* is included in Myrtaceae. The Pteridophytes are treated following Schelpe's (1969) scheme of families and genera. The families of seed plants are listed in Appendix 1 with numbers of genera, species, and endemics. Genera are those admitted by Dyer (1975, 1976) in his revised edition of *The Genera of Southern African Flowering Plants*, with important exceptions listed below. Aizoaceae—genera synonymized by Friedrich (1970), Hartmann (1976), Poppendieck (1976) and Ihlenfeldt & Jörgensen (1973) are not recognized. Liliaceae—minor changes are made with *Poellnitzia* accorded recognition and revisions by Jessop (1970, 1972, 1977) are followed. Restionaceae—following recommendations by Johnson & Evans (1966), Cutler (1969), and Johnson & Briggs (1975, 1978), Gilg-Benedict's (1930) treatment of *Leptocarpus* and *Hypolaena* as exclusively Australasian (the South African species assigned to *Mastersiella* and *Calopsis*) and *Restio* as exclusively African (and Madagascan) is followed. Thus no genera

of Restionaceae are common to Africa and Australia. Cyperaceae—following the arrangement in the Kew Herbarium (after Kükenthal, 1935), *Cyperus* includes *Pycreus*, *Juncellus* and *Mariscus*, while *Schoenoxiphium* is accorded recognition and not placed in *Kobresia*. Compositae—this is much emended including modifications recently published (Nordenstam, 1975, 1976, and in press; Bremer, 1976a, 1976b; Hilliard, 1977; Grau, in press). Campanulaceae—following Thulin (1974, 1975), *Wahlenbergia* includes *Cephalostigma* and *Lightfootia*, while the genus *Unigenes* (Wimmer, 1953) is admitted. Other minor changes made following recent revisions will not be mentioned in detail.

The data in this paper thus constitute a critical compilation assembled from numerous sources and are the only modern presentation of information of this type for southern Africa. Dyer (1975, 1976) provides estimates of numbers of species, and distributions of genera in his generic flora, but is not critical in this respect, and therefore often misleading. It is also noteworthy that in the most recently published estimate of the flora of southern Africa, Killick (1971, 1976) suggests there are somewhat more than 17,000 species while my data indicate that there are about 18,500 species. The figures are of the same order and as studies continue the number will probably be found to lie somewhere between. Numbers in Aizoaceae particularly, are likely to be considerably reduced as more critical revisions such as those of Hartmann (1976), Poppendieck (1976), Ihlenfeld & Jörgensen (1973) appear. There are, however, many species undescribed in South African herbaria (not all accounted for here), as the 45 in Restionaceae illustrate. Even though southern Africa is relatively well collected, an appreciable number of species are still undiscovered as shown by several recent revisions and articles dealing with the flora.

VEGETATION AND PHYTOGEOGRAPHY

Before dealing in more detail with the flora, it is useful to outline some aspects of the vegetation and local phytogeography. There are in fact numerous treatments of the vegetation and its relationships for southern Africa, important works including those of Bolus (1893, 1905), Bews (1925), Pole-Evans (1936), Adamson (1938), and the excellent and detailed work of Acocks (1953). The subject has recently been surveyed in detail by Werger (1978a). Studies relating southern Africa to the continent as a whole are fewer (cf. reviews by Monod [1957] and Werger [1978a]), and of these the recent works of White (Chapman & White, 1970; White, 1976a, 1976b), which have resulted in a revised chorological map of Africa, seem most appropriate in the present context, especially as they are also used by Brenan for tropical Africa (this symposium). White's terminology for phytogeographic zones (Table 2) is followed and, with minor changes in the Cape Floristic Region, also his boundaries for these areas (Fig. 2).

The Cape Region, which forms a major focus in this analysis and is dealt with in great detail, is accordingly defined very closely. While the characteristics of the Cape Flora are generally agreed upon, geographic limits have varied considerably in almost every treatment of note, e.g., Bolus (1905), Pole-Evans (1936), Weimarck (1941), and Taylor (1978). The area here recognized for

TABLE 2. Phytogeographic regions of southern Africa with estimated generic endemism.

Region	Number of Genera
1. Zambezian Region	2
2. Kalahari-Highveld Transition Zone	15
3. Karoo-Namib Region	80 (about 50 Aizoaceae)
4. Tongaland-Pondoland Region	15
5. Afromontane Region	20
6. Cape Region	198

the region is in many ways a compromise, but is based solidly on Acock's definition of the characteristic vegetation type, the fynbos (Fig. 3), and not *primarily* on climate, though it is an area of predominantly winter rainfall.

Some workers have preferred to consider the Cape Flora as the fynbos element only, as this vegetation is the most distinctive and includes the majority of taxa peculiar to the Cape Flora (Oliver, 1977a; Taylor, 1978; White, 1978). Whatever the merits of this position, it is not practical as it prevents simple areal definition with the result that an analysis of the type presented here would be impossible.

Rigid delimitation of White's other phytogeographic zones in southern Africa is very difficult. This is evident in his recognition of the broad Kalahari-Highveld Transition Zone but is also true elsewhere. Definition is difficult in the east between Highveld and Afromontane floras and along the coast between the Tongaland-Pondoland Region and the Afromontane Region. The eastern Cape, a meeting point of four floristic zones, is especially complex and to define this area rigidly without extensive research creates more problems than it solves.

The Cape Region here (Fig. 3) includes all major fynbos areas and extends from Nieuwoudtville in the north, following the eastern slopes of the Cedarberg, and thence east from Karoopoort along the north slope of the Witteberg, Swartberg, Baviaans Kloof, and Groot Winterhoek Mountains, ending at Port Elizabeth. All territory south and west of this line to the coast, containing several other vegetation types, in addition to fynbos, forms the Cape Floristic Region. Simply for convenience a northern limit is drawn at the Olifants River from its mouth to the Giftberg, where it turns south. This specifically excludes small isolated areas of depauperate Cape fynbos north along the west coast of Namaqualand and in the Kamiesberg as well as the western Karoo between Calvinia and Sutherland, i.e., Weimarck's Hantam-Roggeveld subcenter. Also excluded are islands of fynbos in the east on the Groot River Heights and the narrow belt running east–west along the Zuurberg summit in the Albany district, Weimarck's Zuurberg subcenter, which is essentially an area of coastal forest and grassland with a minor fynbos constituent.

FLORISTIC REGIONS

1. *Zambezian Region.*—This region occupies a vast area from southern Zaïre and Tanzania south to Zambia, Angola, Rhodesia and Mozambique to the northern part of Namibia, northeastern Botswana and the northern half of the

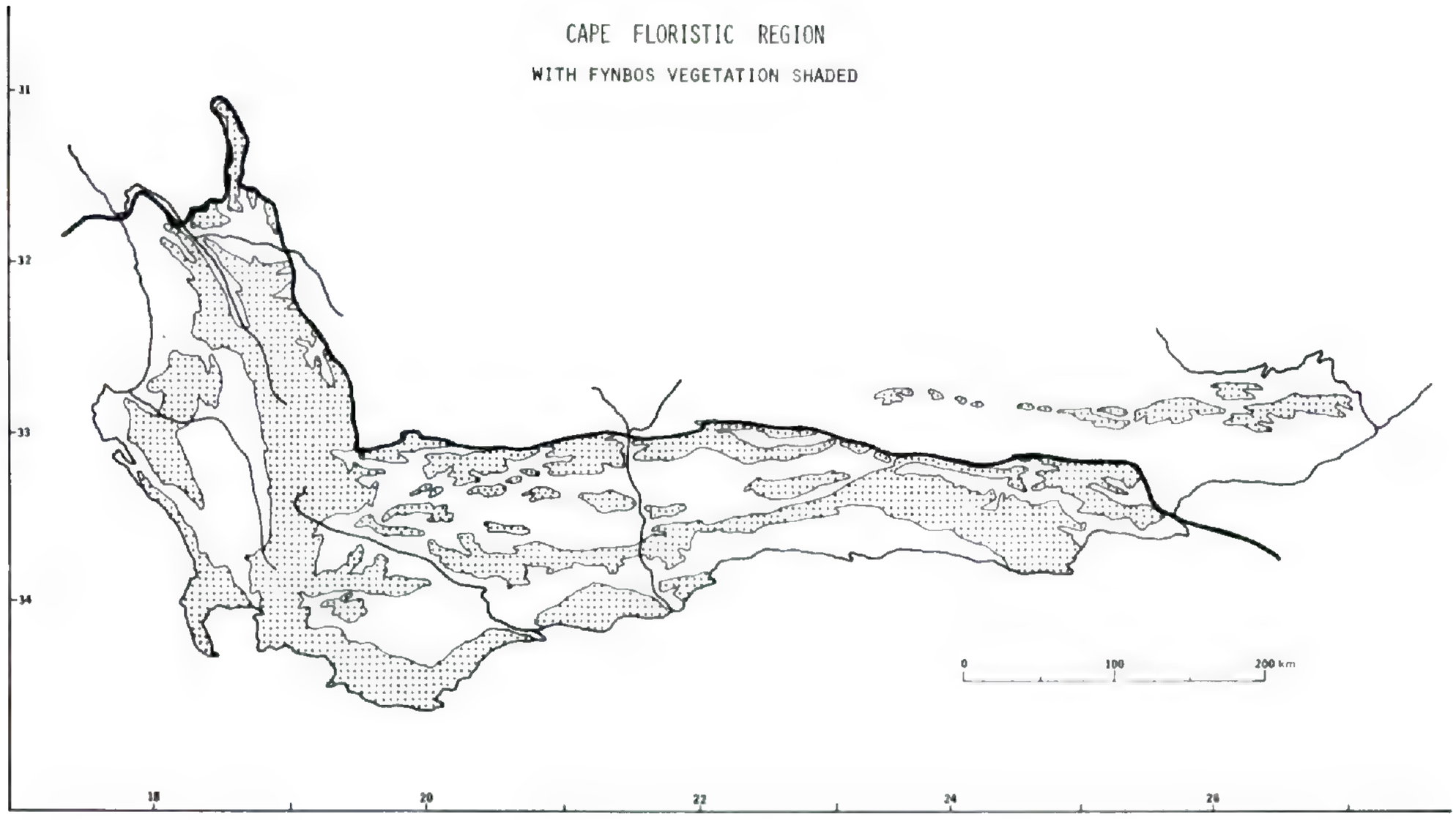

Figure 3. The limits of the Cape Floristic Region as defined in this paper. Areas of fynbos type vegetation [Acock's (1953) Macchia, False Macchia, Coastal Macchia and Coastal Renosterbosveld] shaded.

Transvaal. In brief, it is a tropical area of grassland and open woodland, with Gramineae and woody and shrubby Leguminosae very well represented. The southern portion is relatively depauperate and lacks many characteristic elements. In southern Africa there are only two species of the widespread *Brachystegia* and one of *Julbernardia* (both Leguminosae), while *Tamarindus* (Leguminosae), another very typical Zambezian genus, is not recorded. The single record of *Monotes* and of its family Dipterocarpaceae for southern Africa is in northeastern Botswana. There are perhaps only two genera that are clearly endemic in the southern African portion of the Zambezian Region, *Volkiella* (Cyperaceae) and *Mosdenia* (Gramineae), both monotypic (Table 2).

2. *The Kalahari-Highveld Transition Zone.*—Lying south and west of the Zambezian Region, this region is one of transition from the tropical Zambezian to the arid Karoo-Namib Region. This region is essentially grassland with the minor woody element (*Acacia* is notable), mainly of Zambezian species, often very dwarfed by climate or soil. It is almost exclusively southern African (a small segment lies in southern Angola), and it encompasses the relatively well-watered grasslands of the Transvaal and Orange Free State highveld, as well as the lightly wooded but arid grassland of the northern Cape Province, south and central Botswana, and eastern Namibia including the Kalahari Desert. Although the largest phytogeographic region in southern Africa, it is relatively poor in species and has few endemics, exemplifying its transitional nature. An estimated 15 genera, mostly small, are confined to this region, including *Neuradopsis* (Neuradaceae), *Duthieastrum* (Iridaceae), *Psilochloa* and *Tarigidia* (Gramineae), and several Aizoaceae. Werger (1978a, 1978b) prefers to include the southwestern portion of this transitional region, the southern Kalahari, as part

of the Karoo-Namib Region and the remainder as part of the Zambezian Region. This emphasizes the karoid affinities (Werger, 1973) of many of the more characteristic elements of the Kalahari-Highveld Zone.

3. *The Karoo-Namib Region.*—This occupies the interior of the Cape Province and the entire west coast of Namibia as well as Namaqualand (the northwestern part of the Cape Province). Outside southern Africa the region extends into southwestern Angola. It is entirely arid, desert or semidesert, and has a very characteristic flora. The ecology and vegetation of the region are described in detail by Werger (1978b). The region is diverse and Werger recognizes five subregions. In its eastern portion, which has a summer rainfall, the landscape is dominated by small shrubs, mainly Compositae, with grasses well represented. In the west, with predominantly winter rainfall, there is a wealth of succulents of Aizoaceae, Asclepiadaceae, Crassulaceae, Zygophyllaceae, Geraniaceae, Liliaceae, and Compositae that constitute the greatest development of such plants of any arid or desert flora (Compton, 1929). Annuals often appear conspicuous, but except in the Namib Desert, the southern Kalahari (Leistner, 1967)—included in this region by Werger (1978b)—and in disturbed sites, seldom comprise a high proportion of the species present. The region is the center for Aizoaceae—Mesembryanthemoideae, which have radiated extensively along the west coast. As might be expected, endemism is very high both at species and genus level, and at least 80 genera are endemic or centered in the Karoo-Namib of which some 50 belong to Aizoaceae. Restricted to the region but not to southern Africa are such interesting genera as *Welwitschia*, the peculiar relict gymnosperm, and *Adenolobus*, the caesalpinioid legume perhaps related to the Northern Hemisphere *Cercis*.

In the southern part of this region, wherever rainfall is sufficient, there are isolated pockets of Cape Flora. Acocks (1953) has stressed the close relationship of the Cape and Karoo floras, communities of which are in ecotonal balance. Cape elements contribute significantly to the Karoo-Namib flora, while the few woody emergents have tropical affinities, e.g., *Rhigozum* (Bignoniaceae), *Commiphora* (Burseraceae), *Nymania* (Meliaceae), *Erythrophysa* (Sapindaceae), and *Boscia* (Capparaceae).

4. *The Tongaland-Pondoland Region.*—This is a subtropical forest zone, extending along the coast from the eastern Cape Province to extreme southern Mozambique. It is related to the coastal forests of East Africa (Zanzibar-Inhambane Region) and secondarily to the main African tropical rain forest of the Guinea-Congo Region (see detailed survey by Moll & White, 1978). The Tongaland-Pondoland Region is a mosaic of forest and coastal grassland that interfingers with elements of the Afromontane Region bordering it on the west (White, 1976b). There are many endemic species in the region, but perhaps only about 15 endemic genera; the figure of 23 given by Moll & White (1978) seems rather inflated. The endemic genera of the region, though not necessarily of southern Africa as defined here, include *Rhynchocalyx* (Lythraceae), *Jubaeopsis* (Palmae, which is related to the tropical African *Elaeis*), *Pseudosalacia* (Celastraceae), *Mackaya* (Acanthaceae), *Anastrabe* (Scrophulariaceae), *Bachmannia* (Capparaceae), and *Umtiza* (Leguminosae). The cycad *Stangeria*, the

only genus of Stangeriaceae, is restricted to the region, while Achariaceae is centered here though extending southward as far as Knysna. Several more genera such as *Hippobromus* (Sapindaceae), *Loxostylis* (Anacardiaceae), and *Harpephyllum* (Anacardiaceae) have the main part of the range in the region. Many tropical forest elements occurring in southern Africa are virtually restricted to the Tongaland-Pondoland Region, e.g., *Ptaeroxylon* (Ptaeroxylaceae), *Barringtonia* (Lecythidaceae), *Raphia* (Palmae), *Schlecterina* (Passifloraceae), *Xylotheca* (Flacourtiaceae), *Mitriostigma* (Rubiaceae), *Inhambanella* (Sapotaceae), *Cola* (Sterculiaceae), and the few southern African mangroves, e.g., *Avicennia* (Avicenniaceae), *Ceriops*, *Bruguiera*, and *Rhizophora* (Rhizophoraceae), and *Lumnitzera* (Combretaceae).

5. *The Afromontane Region.*—This is not a discrete region but a series of isolated highland areas, mainly along the eastern half of Africa, with its main centers in Ethiopia, East Africa, and eastern South Africa (White, 1978). In southern Africa it is situated around the Drakensberg Mountains, located mainly in Lesotho and western Natal, where high altitude allows development of an alpine flora which has been described in detail by Killick (1978). It extends northward through the eastern Transvaal and southward to the Hogsback area of the eastern Cape Province. There are characteristic forest taxa, but with the Cape forests excluded from the Afromontane Region here, the southern African Afromontane flora is predominantly a grassland, with a rich herbaceous flora. Species endemism is high and there are perhaps as many as 24 genera endemic or strongly centered in the region, including one family, Greyiaceae, and genera such as *Eumorphia* (Compositae), *Rhodohypoxis* (Hypoxidaceae), and *Bowkeria* and *Glumicalyx* (Scrophulariaceae).

Affinities lie with other Afromontane zones outside southern Africa, and the whole region, which is temperate, shows some relationship with Eurasia, e.g., *Festuca* and *Koeleria* (Gramineae), *Trifolium* (Leguminosae), and *Geum* (Rosaceae). There are also affinities with the Cape Region, and many typical Cape genera extend northward in the Afromontane Region to East Africa, e.g., *Cliffortia* (Rosaceae), *Muraltia* (Polygalaceae), and *Euryops* and *Osteospermum* (Compositae), to mention a few prominent examples (see Weimarck, 1941; Hedberg, 1965). However, many of the typical Afromontane taxa in southern Africa are derived from the surrounding lowland flora (Hilliard, pers. comm.; White, 1978), and floristic relationships of the scattered Afromontane areas are as much with adjacent areas as with more distant highlands.

6. *The Cape Region.*—This region occupies a small area at the extreme southwest of the subcontinent, and has a relatively mild, temperate, Mediterranean type climate. Rainfall is predominantly or entirely in the winter, but the eastern part also receives substantial summer rain. The characteristic vegetation is maquislike (the fynbos) with numerous shrubs or small trees with sclerophyllous or ericoid leaves. The ecology and vegetation of the area has been dealt with extensively by Taylor (1978). The Cape Region as defined here also includes a substantial temperate forest element related to the Afromontane forest, but with some notable endemics, as well as Karoo-Namib elements in the drier valleys. The constituents of the Cape Flora are sharply different from

TABLE 3. Families endemic in southern Africa.[a]

Family	Number of Genera/Species	Distribution
Stangeriaceae	1/1	Southeastern coast, Zululand to eastern Cape
Greyiaceae	1/3	Eastern mountains, Transvaal to eastern Cape
Achariaceae	3/3	Eastern mountains and coast, Transvaal to southern Cape
Bruniaceae	12/75	Southwestern Cape, only 3 species extending east of Port Elizabeth, 1 in Natal
Penaeaceae	7/21	Southwestern Cape, widespread
Stilbaceae	5/13	Southwestern Cape, Ceres to Riversdale
Grubbiaceae	1/3	Southwestern Cape, widespread
Roridulaceae	1/2	Southwestern Cape, Cedarberg to Swellendam
Geissolomataceae	1/1	Southwestern Cape, Langeberg
Retziaceae	1/1	Southwestern Cape, Stellenbosch to Bredasdorp

[a] Other families sometimes accorded recognition are Oftiaceae (1/3—Cape and Namaqualand); Curtisiaceae (1/1—Cape–eastern highlands of Rhodesia); Aitoniaceae (1/1—Little Karoo and Namibia).

those of the other parts of southern or tropical Africa, with high numbers of Proteaceae, Ericaceae, Iridaceae, Rutaceae, Thymelaeaceae, and Restionaceae, as well as Compositae and Leguminosae (only Papilionoideae), whereas Gramineae are relatively unimportant. Similarities in family composition in western Australia have often in the past prompted suggestions of a floristic relationship with the Cape Region. As Adamson (1958) has pointed out, differences are stronger than the similarities, and the Proteaceae, Rutaceae, Leguminosae, and Restionaceae of the two areas have entirely different and independent origins.

Not only is the Cape Region remarkably rich in species, but it has unusually high endemism for a continental area, in fact approaching the levels for species[4] encountered in Australia, Hawaii, and New Zealand (Table 1). Some 198 genera are endemic in the Cape Region and another 40 at least are centered here with minor extensions in adjacent areas. Eight of the ten families endemic in southern Africa occur in the Cape Region and six of these are restricted entirely to it (Table 3).

SURVEY OF FAMILIES, GENERA, SPECIES, AND ENDEMISM

ENDEMIC FAMILIES

As many as 14 endemic families have been recognized in southern Africa (Brenan, this symposium), although only ten are included here (Table 3). This compares with nine families endemic in tropical Africa (Brenan, this symposium), while three families are shared between southern and tropical Africa (Oliniaceae, Welwitschiaceae, and Melianthaceae and, if recognized, also Heteropyxidaceae, Wellstediaceae, Kirkiaceae and Curtisiaceae). The ten southern African endemic families, including 123 species, are all found in the well-watered parts of southern Africa, from the coastal belt and eastern escarpment to the mountains of the southwestern Cape. Six are in fact restricted to the

[4] Different estimates of endemism quoted by Weimarck (1941) and others are mainly due to different geographical definitions of the Cape Region, but more extensive collecting recently has extended the known ranges of several genera and species.

Cape Region, and Bruniaceae are centered here, with minor extensions to the east. These endemic Cape families are all shrubs of the fynbos, which occur mainly in montane habitats. Of the endemic families of southern Africa, only Greyiaceae and Stangeriaceae do not occur in the Cape Region, the former centered in the eastern mountains, whereas Stangeriaceae is restricted to the Tongaland-Pondoland Region.

In addition to the ten endemic families, Oftiaceae (1/3 Cape and Namaqualand) is sometimes accorded recognition, but is regarded here as Scrophulariaceae, though originally placed in Myoporaceae (Dahlgren & Rao, 1971; Goldblatt, 1976a; Leroy, 1977). Curtisiaceae (1/1 southwestern Cape and eastern highlands of Rhodesia) has also recently been accorded family status, though traditionally treated as Cornaceae—Curtisioideae (Eyde, 1967; Takhtajan, 1973; Goldblatt, 1978). Curtisioideae does not appear as closely related to Cornaceae as several other currently recognized families of this alliance. Aitoniaceae, with the monotypic *Nymania*, has been firmly assigned to Meliaceae (Pennington & Styles, 1975).

Affinities of Achariaceae are with Passifloraceae; Stilbaceae, almost certainly with Verbenaceae; Greyiaceae possibly with Melianthaceae or Sapindaceae, and Penaeaceae perhaps with Oliniaceae (Levyns, 1964) or Melastomataceae—Memecyloideae (Dahlgren, unpubl.) and certainly Myrtales. Relationships of the remainder are problematic. Retziaceae is perhaps related to Loganiaceae, especially Buddleieae (Leeuwenberg, 1964; Herbst, 1972; Goldblatt & Keating, 1976) or to Stilbaceae (Dahlgren et al., 1979). It is clearly a relict, even if distantly related to Loganiaceae. Bruniaceae, Roridulaceae, Geissolomataceae, and Grubbiaceae appear to have no close relatives. All are shrubby in habit with small to ericoid leaves. They are morphologically and anatomically unspecialized (Carlquist, 1975, 1976, 1977) and may be derived from an archaic southern African stock. They do not resemble one another closely, yet may be distantly allied; and they have been grouped in Pittosporales, a predominantly Austral order, by Thorne (1975, 1976), together forming the African-Madagascan suborder Bruniineae. Carlquist has shown that these families, all with relatively unspecialized wood anatomy, have no internal adaptations for xeric habitats. In fact, though found in a region of Mediterranean climate with summer drought, most species actually grow in moister situations often with summer moisture from cloud condensation or in marshes or seeps. They certainly appear to be mesophytic relicts surviving in wet montane habitats in a subarid region, as Carlquist (1976) has suggested.

A few families, although not strictly endemic, merit mention here as they have the majority of their taxa in southern Africa, and are centered in the southern or southwestern part of the subcontinent. These include Aizoaceae which in southern Africa has 135 genera, of which 113 are endemic, and slightly more than 2,000 species, of which 98% are endemic. As treated here, Aizoaceae includes Mesembryanthemaceae, Molluginaceae and Tetragoniaceae. Selaginaceae (10/ca. 215), also primarily southern African with a few species in East Africa and Madagascar, is related to Scrophulariaceae and to the Mediterranean Globulariaceae. All ten genera occur in southern Africa and some 204 of the esti-

TABLE 4. Ranking of families in the southern African flora by size. Percentage figures are of the total flora.

	Number of Genera	Endemic Genera		Number of Species	Endemic Species	
1. Compositae	174	80	Compositae	2,072	1,801	30%
2. Gramineae	167	23	Aizoaceae	2,020	1,896	
3. Aizoaceae	135	113	Leguminosae	1,495	1,114	
4. Leguminosae	115	20	Liliaceae	907	803	51%
5. Asclepiadaceae	60	21	Iridaceae	840	816	
6. Rubiaceae	59	8	Ericaceae	799	797	
7. Liliaceae	54	21	Gramineae	743	330	
8. Orchidaceae	54	15	Asclepiadaceae	605	526	
9. Scrophulariaceae	51	14	Scrophulariaceae	515	447	
10. Iridaceae	44	27	Orchidaceae	461	371	
11. Acanthaceae	41	6	Cyperaceae	421	218	
12. Euphorbiaceae	41	4	Euphorbiaceae	389	310	
13. Umbelliferae	32	12	Campanulaceae	380	350	
14. Labiatae	31	2	Acanthaceae	355	236	
15. Cyperaceae	30	7	Proteaceae	336	326	
16. Ericaceae	24	19	Restionaceae	316	316	
17. Rutaceae	23	13	Geraniaceae	271	261	
18. Amaranthaceae	20	3	Rutaceae	270	255	
19. Campanulaceae	18	12	Rubiaceae	234	122	
20. Amaryllidaceae	17	10	Labiatae	225	161	
			TOTAL	13,682	(74%)	

mated 210 species are endemic. Recently Hilliard & Burtt (1977) and Burtt (1977) have pointed out that Selaginaceae are as closely related to Scrophulariaceae—Manuleeae as the latter are to other tribes of Scrophulariaceae, and they therefore recommend treating Selaginaceae as a tribe of Scrophulariaceae.

SURVEY OF LARGER FAMILIES

The largest families are Compositae (2,072 species) and Aizoaceae (2,020 species) (Table 4). The latter, centered in southern Africa, are in need of critical revision and probably comprise considerably fewer species than currently recognized. Problems associated with the systematics of Aizoaceae, and succulents in general, are well known (Cole, 1969; Raven, 1970) but are gradually being resolved by critical research. Nevertheless, Aizoaceae is a major family in this region, and very characteristic of the flora of the arid parts of the subcontinent. Both Compositae and Aizoaceae exhibit an extraordinary degree of endemism, both above 85%; together they comprise nearly 30% of the species in southern Africa. The high endemism was noted very early in Compositae by Bentham (1873), who also drew attention to the relictual nature of many southern African members of this family. Leguminosae is third largest, with 1,495 species, 1,114 of which are endemic (74%). This family, though fundamentally a tropical one, shows a great development in Crotalarieae and Liparieae (tribes circumscribed after Polhill, 1976) concentrated in the Cape Region, where such genera as *Aspalathus* (255 species), *Rafnia* (22 species), *Priestleya* (18 species),

TABLE 5. Ranking of families in the Cape Floristic Region with the largest genus in each family and its percentage of the total for the family.

Family	Number of Species	Largest Genus	Number of Species	%
1. Compositae	1,034	*Senecio*	122	11.9
2. Ericaceae	765	*Erica*	605	79.1
3. Aizoaceae	728	*Ruschia*	134	18.4
4. Iridaceae	624	*Gladiolus*	71	11.4
5. Leguminosae	606	*Aspalathus*	253	41.7
6. Liliaceae	369	*Lachenalia*	55	14.4
7. Proteaceae	322	*Leucadendron*	80	24.8
8. Restionaceae	315	*Restio*	137	43.5
9. Rutaceae	250	*Agathosma*	130	52.0
10. Campanulaceae	242	*Wahlenbergia*	77	31.8
11. Orchidaceae	220	*Disa*	42	19.1
12. Cyperaceae	203	*Ficinia*	57	28.1
13. Scrophulariaceae	194	*Sutera*	34	17.5
14. Gramineae	154	*Pentaschistis*	30	19.5
15. Geraniaceae	150	*Pelargonium*	138	92.0
16. Rhamnaceae	139	*Phylica*	136	97.8
17. Polygalaceae	133	*Muraltia*	106	79.7
18. Oxalidaceae	127	*Oxalis*	127	100.0
19. Thymelaeaceae	127	*Gnidia*	48	37.8
20. Rosaceae	115	*Cliffortia*	109	94.8

and *Amphithalea* (15 species) are centered. The development of Leguminosae is mainly in Papilionoideae, which has 1,365 species, while Mimosoideae and Caesalpinioideae have only 75 and 55 species respectively.

There are six families with between 500 and 1,000 species: in order of size, Liliaceae (950 species), Iridaceae (840 species), Ericaceae (822 species), Gramineae (743 species), Asclepiadaceae (605 species), and Scrophulariaceae (515 species). Two of these, Liliaceae and Iridaceae, together with Orchidaceae (461 species), form the major part of the wealth of geophytic, petaloid monocots so characteristic of the southern African flora. These three petaloid monocot families together comprise over 12% of the flora, a unique situation, with floras of other semiarid parts of the world having a much poorer representation of petaloid monocots.

Gramineae, with some 743 native species, is an important element of the flora. Some 330 are endemic species (44%). It shows stronger relationships with the tropical African flora than other large families. Gramineae is poorly represented in the Cape Region compared to many other families, with some 154 species, only 68 of which are endemic. Most Cape grasses belong to Danthonieae, a tribe with a distinct Austral distribution.

The families for which southern Africa, particularly the Cape Region is so well known, Proteaceae (336 species), Restionaceae (316 species), Geraniaceae (271 species), and Ericaceae (822 species) are all centered in the southwestern portion of Africa and contribute substantially to the size of the flora, though they are poorly represented outside the Cape.

In the Cape Region, family composition is somewhat different (Table 5).

Compositae is still largest (1,034 species), followed by Ericaceae (765 species), Aizoaceae (728 species), Iridaceae (624 species), and Leguminosae (606 species). The petaloid monocot families—Iridaceae, Liliaceae, and Orchidaceae—comprise 1,213 species, or nearly 15% of the total flora. If Amaryllidaceae, Haemodoraceae, Tecophilaeaceae, and Hypoxidaceae are included, petaloid geophytic monocots account for 1,336 species, 16% of the Cape Flora, and for two-thirds of the monocots of this flora, a situation that appears unparalleled anywhere in the world.

The very characteristic families, Proteaceae and Restionaceae, assume importance in terms of number of species in the Cape Region, far exceeding Graminae, Euphorbiaceae, and Asclepiadaceae, which are more tropical families that are well represented in southern Africa as a whole. Some of the larger Cape families listed exhibit a pattern of one very large genus and few other species (Table 5). More than half the family Rutaceae consists of species of *Agathosma*, and this pattern is even more accentuated in *Phylica*, with 136 species of 139 Rhamnaceae, *Muraltia*, with 106 species of 133 Polygalaceae, *Cliffortia*, with about 109 species of 115 Rosaceae, and *Pelargonium*, with 138 species of 150 Geraniaceae. All 127 species of Oxalidaceae in the Cape Region belong to *Oxalis*.

ENDEMIC GENERA

For southern Africa as a whole some 560 of 1,930 native genera are endemic (29%). These are listed in Appendix 2 with ranges and numbers of species. A further 50 genera at least have the majority of their species or distribution in southern Africa, with a few species extending locally into tropical Africa. Some examples of this pattern are *Anastrabe* and *Manulea* (Scrophulariaceae), *Harpephyllum* (Anacardiaceae), *Putterlickia* (Celastraceae), *Dimorphotheca*, *Leontonyx*, *Othonna*, *Pteronia* and *Sphaeroclinium* (Compositae), *Craterocapsa* (Campanulaceae), *Leucosidea* (Rosaceae), and *Curtisia* (Cornaceae). *Cliffortia* (Rosaceae) and *Muraltia* (Polygalaceae), each with over 100 species in the Cape Region, extend through eastern South Africa with a few species reaching as far as East Africa (Table 11). This pattern is mirrored in several smaller genera also: for example, *Moraea*, *Hesperantha*, *Dierama* (all Iridaceae), *Hebenstreitia* and *Selago* (Selaginaceae), *Euryops* and *Felicia* (Compositae). A few genera, including *Leyssera*, *Ifloga*, *Lasiopogon*, *Lasiospermum*, *Osteospermum* (Compositae) and *Gynandriris* (Iridaceae), are essentially southern African, with a single species also occurring in the Mediterranean area or Middle East (Table 11).

Of the endemic genera, 198 are restricted to the Cape Region and at least another 50 are centered in this area with very minor extensions outside the Cape (Table 2). A second important center of endemism is the Karoo-Namib Region with some 80 endemic genera, 50 of which belong to Aizoaceae—Mesembryanthemoideae. The Afromontane areas of southern Africa also form an important center with some 20 genera endemic or concentrated here. Boundaries of this region are often indistinct with much interfingering in the east and west with adjacent floristic zones. In the Tongaland-Pondoland Region there are perhaps

TABLE 6. Ten largest genera in southern Africa and in the Cape Region with percentage of the total flora.

Southern Africa			Cape Region	
1.	*Erica* (Ericaceae)	635	*Erica* (Ericaceae)	605
2.	*Ruschia* (Aizoaceae)	326	*Aspalathus* (Leguminosae)	253
3.	*Senecio* (Compositae)	285	*Pelargonium* (Geraniaceae)	138
4.	*Aspalathus* (Leguminosae)	255	*Restio* (Restionaceae)	137
5.	*Helichrysum* (Compositae)	245	*Phylica* (Rhamnaceae)	136
6.	*Euphorbia* (Euphorbiaceae)	235	*Ruschia* (Aizoaceae)	134
7.	*Pelargonium* (Geraniaceae)	213	*Agathosma* (Rutaceae)	130
8.	*Conophytum* (Aizoaceae)	210	*Oxalis* (Oxalidaceae)	127
9.	*Indigofera* (Leguminosae)	209	*Senecio* (Compositae)	122
10.	*Oxalis* (Oxalidaceae)	201	*Cliffortia* (Rosaceae)	109
	TOTAL	2,822 = 15.3%	TOTAL	1,891 = 22.3%

15 endemic genera. Some 15 genera are restricted to the Kalahari-Highveld and only 2 to the southern African part of the Zambezian Region.

In terms of numbers of endemic genera, Aizoaceae is the most important family with 113 in southern Africa, all but five belonging to Mesembryanthemoideae, which is centered in the arid regions of the southwest. Compositae has 80 endemic genera, best represented in Inuleae and Anthemideae, as well as in Calenduleae and Arctotideae, which are centered in the south and west. Petaloid monocots form another major group with Iridaceae having 27 of 44 genera endemic, Liliaceae 22 of 56 and Amaryllidaceae 10 of 17, southern Africa being the center for Iridaceae—Ixioideae and for Amaryllideae. Other important groups are Gramineae with 23 endemic genera if the segregates of *Danthonia* are accepted, as they are here, otherwise only 20; Asclepiadaceae with 21 endemic genera; Ericaceae 19; Scrophulariaceae 16; Orchidaceae 15; Umbelliferae 12; Restionaceae 11; and Proteaceae 10.

Clearly, massive evolutionary radiation in a number of isolated herbaceous and woody monocot and dicot genera is a characteristic feature of the southern African flora. This has resulted in the development of several very large genera in the flora, and in a remarkably high species per genus ratio. Ten genera in southern Africa have over 200 species (Table 6). The largest is *Erica* with some 635 species, mostly found in the Cape Region as are the other genera except *Ruschia*, which is widespread in arid areas. The number of species in the 10 largest genera in southern Africa is 2,799 or 15.3% and for the Cape Region alone, 1,891 or 23.3%. In terms of genus per species ratios (Table 3), the figure for southern Africa is 7.7 and for the Cape Region 8.9, both remarkably high on a world scale (Table 7).

ENDEMIC SPECIES

Of the approximately 18,500 native species in southern Africa about 14,820 (80%) are endemic, a percentage unusual for a continental area. Similar proportions of endemism are mainly associated with whole isolated land masses such as Australia (ca. 85%), New Zealand (ca. 81%), Hawaii (ca. 92%). The

TABLE 7. Selected statistics for parts of southern Africa and various comparable regions, with the ten largest genera, monocots, Compositae and annuals as percentage of total flora.

Region	Species per Genus	Ten Largest Genera	Monocots	Compositae	Annuals
Southern Africa	7.7	15.1	23.0	11.0	7.0
Cape Region	8.9	22.1	24.2	11.9	6.4
Cape Peninsula[a]	4.2	17.5	34.6	11.5	9.6
Natal[b]	3.9	17.0	27.1	11.4	6–7
Gray's Manual Area[b] (Eastern North America)	5.2	21.8	28.2	12.7	8.7
Europe[c] (*Flora Europaea*)	7.8	14.0	18.0	12.0	?
California Floristic Province[a]	5.6	15.2	19.2	13.6	27.4
Carolinas[a]	3.5	14.5	23.6	10.4	3.8
Sonoran Desert[a]	3.3	12.8	12.1	15.0	21.4
Texas[a]	3.9	10.2	24.4	13.4	20.4
Hawaii[a]	7.5	42.1	8.5	11.4	0.04
New Zealand[a]	7.4	26.3	27.3	12.5	6.0

[a] Data from Raven & Axelrod (1978).
[b] Data from Ross (1973), with estimate of annuals from Bews (1916) a figure "including many not native."
[c] Webb (1978), including introduced taxa.

very high percentage of endemism in southern Africa supports the contention that this region forms a coherent unit, however artificially the boundaries may appear to have been drawn. The level of endemism also emphasizes the degree to which the southern African region has evolved in isolation for a considerable period of time. Following the example of Raven & Axelrod (1978) aspects of species and generic endemism will be discussed in relation to statistics presented in Table 7.

As already mentioned in discussing generic endemism, southern Africa has a very high number (7.7) of species per genus, while the Cape Region, the only local area for which I have been able to provide data, has 8.9 species per genus (Table 7, column 1). These figures are striking and are approached only by the islands of New Zealand and Hawaii as well as by the very large *Flora Europaea* area. As elaborated by Raven & Axelrod (1978) in relation to the California Floristic Province (where there are 5.6 species per genus), high levels such as these suggest major bursts of speciation in isolated genera which thus contribute very unevenly to the flora. The Cape Region appears quite exceptional in this respect and southern Africa somewhat less so, although the figure here includes the Cape Region. However, even with the Cape Region excluded, there are some 7.1 species per genus in southern Africa, indicating that major episodes of speciation have played a significant role here too.

As regards percentage of total flora included in the ten largest genera—second column of Table 7—southern Africa appears unexceptional (15.1%) while the Cape Region (22.1%) has a relatively high proportional contribution from a few genera, approaching the situation in New Zealand (26.3%), but nothing like Hawaii, for example, with 42.1%.

Both the proportion of monocotyledons and contribution of Compositae to the total flora, in southern Africa as a whole and the Cape Region, appear unremarkable. Usual proportions of monocotyledons range around 25%, while Com-

positae generally constitute 10–12% of a flora with a somewhat lower figure for moist tropical areas. The fact that the proportion of monocotyledons is normal in the Cape is surprising since in the Cape Peninsula, a small part of the Cape Region, monocotyledons comprise some 34.6% of the flora (Adamson & Salter, 1950; Raven & Axelrod, 1978). An explanation for the richness of monocots on the Cape Peninsula is not known but may lie partly in that this area is particularly well watered and has more than the usual marshy situations, conditions where, at least in the Cape, there are more species of Restionaceae and Cyperaceae as compared to drier areas. In terms of the monocot families represented, southern Africa, and especially the Cape, are extraordinary with 14% and 16% petaloid monocots respectively.

The last column of Table 7 indicates that southern Africa, including the Cape, has very few annual species in comparison to the total flora. There are some 1,308 annuals in southern Africa (7%) and an estimated 550 in the Cape Region, only 6.4%. Comparable areas for which this information is available (Raven & Axelrod, 1978), such as the California Floristic Province (27.4%), and the State of California (28.6%) have many more annuals proportionately, as do other arid or semiarid areas, especially those with arid climates and moist winters (Raunkiaer, 1934). Figures are not available for many other parts of the world with a Mediterranean climate except for the Mediterranean vegetation of Palestine (Orshan, 1953), which, with 30% annuals, appears comparable to California. Examples given by Raunkiaer for local lowland areas in Greece, Italy, and elsewhere in the Mediterranean suggest even higher proportions of annuals. In general annuals appear to comprise a high proportion of floras in warm semiarid to arid areas with winter rainfall, and particularly in the Old World in the Mediterranean and the Middle East (Raunkiaer, 1934; Raven & Axelrod, 1978). In southern Africa the reasons associated with the low proportion of annuals require investigation. Low frequencies of annuals have also been noted by Bews (1916) for Natal, 6–7%, by Compton (1929) for the arid Whitehill flora of the western Karoo, 11%, by Adamson (1927), 5–7%, and by Cody & Mooney (1978) for Jonkershoek, a small area in the Cape Region. A high frequency of annuals has been recorded in southern Africa for the southern Kalahari (Leistner, 1967) where 33% of the 444 species in this flora are annual.

The southern African annuals are predominantly dicots (Table 8) with Cyperaceae (40 annuals), Liliaceae (1 annual), Gramineae (ca. 150 annuals), Juncaceae (6 annuals), Commelinaceae (4 annuals), contributing to a total of some 205 annual monocots or only about 15.8% of the total 1,297 annuals (one of which, *Selaginella pygmaea*, is a Pteridophyte). This differs somewhat from the situation Raven & Axelrod (1978) describe in California where of a total of 1,098 annual species only 85 (7%) are monocots. Dicots are better developed in California generally but especially so are annuals: there are more annual dicots in California than in all southern Africa. Among the southern African dicots Compositae (235), Aizoaceae (135), and Scrophulariaceae (192) contribute strongly to the annual flora, as well as Campanulaceae (53) and Leguminosae (51). The greatest generic contributions to annual species come from *Nemesia* (50), *Polycarena* (36), and *Diascia* (32) (all Scrophulariaceae) and

TABLE 8. Families of southern Africa and the Cape Region with the largest number of annual species.

Southern Africa		Cape	
Compositae	235	Compositae	122
Scrophulariaceae	192	Scrophulariaceae	106
Gramineae	150	Aizoaceae	60
Aizoaceae	135	Campanulaceae	33
Campanulaceae	53	Cruciferae	32
Leguminosae	51	Crassulaceae	22
Cruciferae	42	Cyperaceae	22
Cyperaceae	40	Gramineae	20
Selaginaceae	31	Selaginaceae	18
Gentianaceae	29	Gentianaceae	17

from *Senecio* (ca. 33) (Compositae) and *Wahlenbergia* (ca. 30) (Campanulaceae). In the Cape Region there are only some 52 annual monocots, 9.5%, of the total annual flora. The decrease in proportion of annuals is due to the paucity of annual grasses in the Cape where annual dicots are better represented proportionately than in southern Africa.

GEOGRAPHICAL AND PALEOBOTANICAL SETTING

Southern Africa is unusually rich in native vascular plants compared with other temperate regions of comparable size and with portions of tropical Africa, and far exceeds any area of similar size in degree of endemism. The Cape Region, for its small size, has a particularly large flora, comparable in numbers of species with some of the richest areas of the Neotropics (Table 1). It has a level of endemism far in excess of any tropical area of comparable size.

The principal reasons for the wealth of species in southern Africa are the following. *First*, environmental diversity is great due to high relief, with humid coastal forest in the east, giving way to a large montane belt, a high interior plateau dipping westward and becoming progressively more arid to form the Karoo and the Kalahari Desert, while the western coastal belt forms the extremely arid Namib Desert. The south and southwest are very mountainous and dry valleys alternate with well-watered mountain belts. *Second*, two entirely different climatic regimes prevail, with summer rainfall/winter drought in the north, east, and interior, and winter rainfall and summer drought in the southwest, while the eastern part of the south coast essentially receives rain all year and has an equable maritime climate. *Third*, recurrent climatic fluctuations since the mid-Pliocene stimulated speciation in plants suited to a region of diverse topography, predominantly arid climate, and diverse soil types. *Fourth*, numbers of relicts have survived in sheltered pockets of equable climate along the coasts, in both summer and winter rainfall areas. Though no analysis of relict plant groups has been made for southern Africa, Adamson (1948) makes a point of their significance. There are clearly many species in this category to be found wherever favorable conditions persisted throughout the extreme arid phases of the Pliocene and Quaternary, including all of the endemic families of the Cape Region.

These conditions are to a greater or lesser degree shared by all areas of semiarid and Mediterranean climate, and most of them have relatively high numbers of species and high endemism. Southern Africa, however, seems exceptional, and the Cape Region is particularly remarkable. Reasons for this are not at all clear. It remains to be demonstrated that southern Africa is more diverse geographically, edaphically or climatically, or whether more relicts are located here than in comparable areas. In one condition, however, southern Africa does differ from other regions. The Mediterranean and arid belts form the southern tip of the continent with no temperate land extension polewards, as there is in North and South America and in Eurasia.

This geographical situation has been used to explain some of the richness and endemism in the extreme south (Thiselton-Dyer, 1909). The so-called *cul-de-sac* theory envisages the flora of the southwest as having evolved in relative isolation from the rest of Africa, but being at the same time also an end point for successive southward waves of plant migration. This idea of large numbers of species accumulating at the end of the continent is unsatisfactory and has been widely rejected (Bews, 1925; Adamson, 1948: 461). However, the extraordinary level of endemism found in southern Africa and the Cape is explicable to some extent by its geographic situation. There is no cool temperate flora extending south with which some species might be shared, as there is in the Mediterranean climate belts of California, Chile, and the Mediterranean basin.

LANDSCAPE

Much of southern Africa consists of an elevated rolling plain with an average altitude of 1,500 m. The plain is broken abruptly in the east and south by steep escarpments and mountain belts. More exactly, from the Transvaal to the eastern Cape the surface is built up of a series of steplike escarpments with the interior plateau a continuation of the summit of the last escarpment. The Cape mountains in the south and southwest are true mountains, consisting basically of much folded strata subsequently faulted in complex fashion (du Toit, 1954). The Cape Region thus consists of several steep mountain chains lying parallel to the coast behind one another, separated by long valleys (King, 1967).

The interior plateau dips gradually to the west where the coastal escarpments are less developed and the rivers draining the central and eastern interior all run the longer distance to the west coast. The Karoo and the Kalahari are arid interior basins of the plateau. The coastal plain on the west coast is also narrow, and with the cold Benguela Current alongside, forms the extremely dry Namib Desert, extending from just south of the mouth of the Orange River to southern Angola.

SOILS

Without going into detail about soil types in southern Africa, it is necessary to mention some peculiarities which are important in floristic considerations. The infertile, acidic and coarse grained siliceous soils derived from sandstones of the Cape System are particularly unusual and closely associated with sclerophyll vegetation. These sandy soils are found mainly in the Cape Region and

extend along the south coast locally to Natal. The most characteristic elements of the Cape Flora are found on this substrate, and many Cape taxa extending east of the Cape Region grow only where these sandy soils occur.

In the Cape Region the mountains are mostly sandstone and the valleys and flats shale. The dissected topography here has its counterpart in a mosaic of two sharply different soil types which help explain the richness and variety of the flora, as many taxa are partly or entirely restricted to one major soil type. This situation, though well known, has not been studied in detail, and most recent monographs acknowledge its importance, e.g., Rourke (1972) for *Leucospermum*; Williams (1972) for *Leucadendron*; Goldblatt (1976b) for *Moraea*; while Dahlgren (1968) has dealt with edaphic factors in detail for *Aspalathus*.

Limestone outcrops are local and also sustain important differences in the flora. Limestone in the southern Cape in particular has characteristic endemic species, a fact emphasised by Muir (1930), who lists the flora of the limestone hills near Riversdale, Weimarck (1941: 62), Acocks (1953), and others. The recent studies of Dahlgern (1968), Rourke (1972: 182), Williams (1972: 397), and Milewski (1977) also mention the significance of limestone substrates for particular plants.

Extensive outcrops of serpentine and other peculiar mineral rich soils occur in southern Africa (Wild, 1978), especially in the Transvaal, but also in Swaziland, Botswana, and Namibia. In many parts of the world such substrates often harbor distinct plant communities and endemic taxa, and serpentine endemics are particularly important in the California flora (see Raven & Axelrod, 1978, for survey). In tropical Africa where Shaba (Zaïre) and Rhodesia have been investigated extensively (Wild & Bradshaw, 1977; Wild, 1978), there are numerous characteristic taxa on copper, nickel, and cobalt rich soils and several species endemic on such soils. In Rhodesia, which has large serpentine outcrops, Wild (1965, 1968) has recorded at least 320 tolerant species and 22 endemics. In contrast, virtually nothing is known about the flora of serpentine and other anomalous soils in southern Africa. It remains to be seen whether there are any taxa or communities characteristic of such soil types, but in the light of much information from elsewhere in the world, including adjacent south tropical Africa, serpentine and other ultrabasic soils would seem likely to be responsible for some of the plant diversity of southern Africa.

CLIMATE AND RAINFALL

In summer, most of southern Africa receives rainfall from moist air flowing from the Congo as the intertropical convergence moves southward. Convectional and orographic precipitation occur, highest in the northeast and diminishing in the center and south (Griffiths, 1972). The cold north-flowing Benguela Current off the west coast controls the climate of the western subcontinent to a large extent (van Zinderen Bakker, 1975; Tankard & Rogers, 1978). This current, which wells up near Cape Town, has a drying effect along the whole coast as far north as the equator, with the resulting high pressure belt over the west coast and south Atlantic inhibiting the flow of moist tropical air westward.

In winter, a second weather system brings moisture-bearing air from the

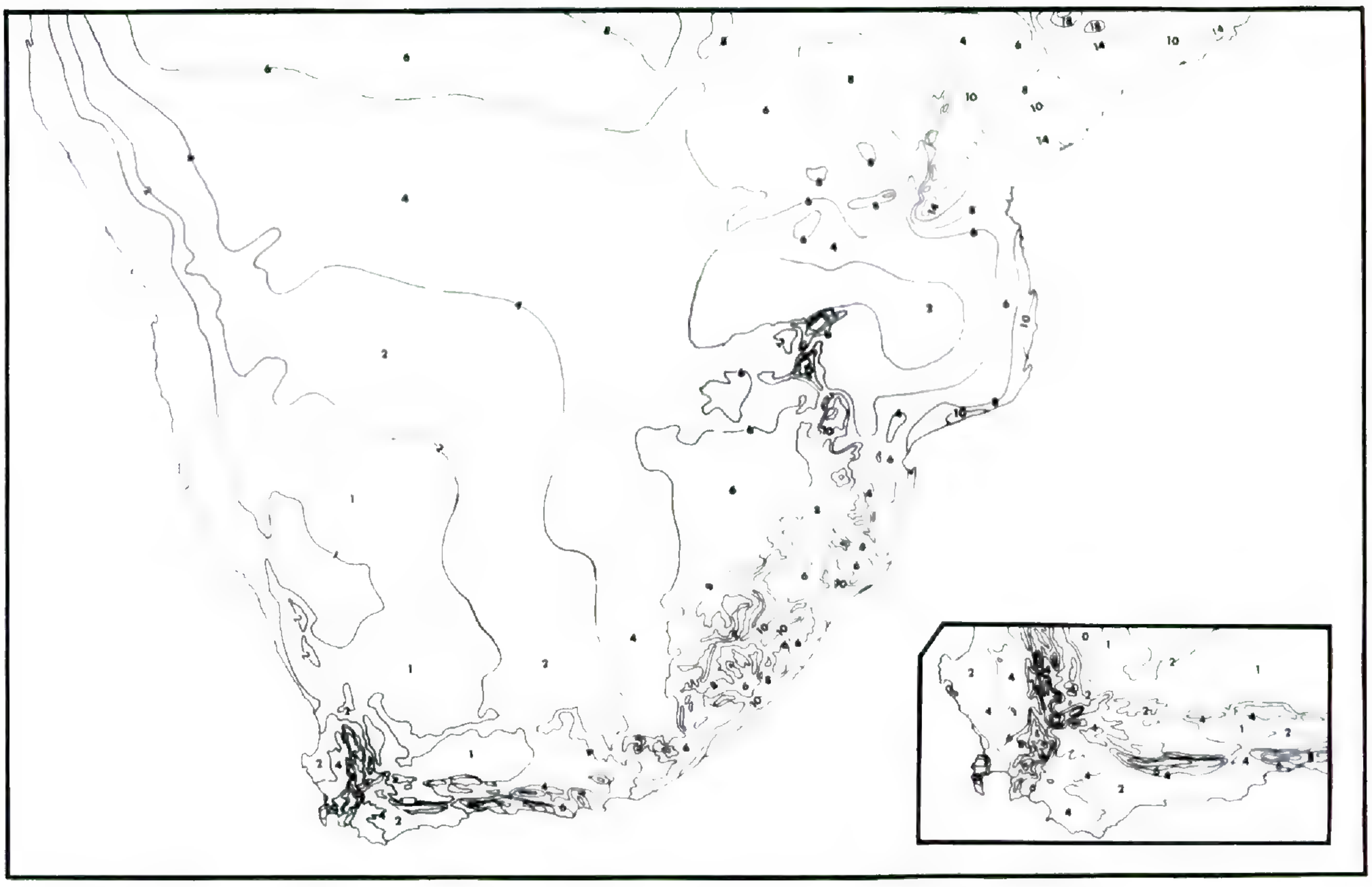

FIGURE 4. Annual rainfall in southern Africa after Jackson (1961). Figures refer to 100 mm of rainfall.

west as the south Atlantic anticyclone moves some 4° equatorward and northwesterlies provide cyclonic and orographic rain to the west coast south of about latitude 28° and to the southern coast. Winter cyclone-produced cold fronts also bring some snow in higher regions of the interior. The climate of the southwest and south coast with summer drought and cyclonic winter rainfall is thus typically mediterranean.

The southeast trade winds of the Indian Ocean have local effects on the prevailing pattern as they bring some rain to the coast and seaward slopes of the mountains. This affects the Cape Region as well, with summer mist or rain produced as far west as Cape Town. These winds play a significant role on the west coast in shifting warmer surface water away from the coast, thus amplifying the upwelling of the Benguela Current.

In terms of measurable precipitation (Jackson, 1961) the mountains of the Cape Region, especially in the southwest, are wettest, with 1,000–1,800 mm falling mainly in winter but also with appreciable summer rain and cloud condensation (Fig. 4). In the lowland areas of the Cape, rainfall is much lower, about 400–500 mm with little summer precipitation. Rainfall in the Namib Desert on the west coast is less than 100 mm per annum. This increases to the east, with most of the Karoo and Namaqualand in the northern Cape Province receiving between 100 and 250 mm per annum. The Kalahari-Highveld is wetter with 350–600 mm, with even more towards the eastern highlands. The highlands and eastern escarpment receive 600–1,000 mm, with 1,400 mm locally and the mean for the southeastern coast ± 900 mm, distributed mainly in summer.

The climate of the region is thus predominantly arid to semiarid, with rela-

tively mesic conditions prevailing only in the eastern third of southern Africa as well as along the southern coast. Although the region lies partly in the tropics, its high elevation, with dryness and widespread frost in winter, result in much of its flora being strongly seasonal with growth in the warm months. This pattern is reversed in the west and south which have a Mediterranean climate with mild, wet winters and relatively dry summers. Between the fairly well-watered eastern and southwestern parts of southern Africa, there are three distinct desert or semidesert areas: the summer rainfall subtropical Kalahari, the summer rainfall temperate Karoo, and the winter rainfall Namib-Namaqualand belt.

PALEOBOTANICAL OUTLINE

It is difficult to judge, except in general terms, the effects of the geological past on the flora of the subcontinent. The fossil record for plants in Africa generally, but especially in the south, is poor from the Jurassic until the Quaternary (Plumstead, 1969). Thus there is a great gap during the time that the angiosperms evolved and became dominant during the Cretaceous, this gap extending until the Pliocene. An excellent study of this period by Axelrod & Raven (1978) surveys the entire Late Cretaceous and Tertiary for Africa. Their critical analysis of the few fossil floras available in the light of plate tectonics and evidence from other parts of the world has produced a generalized picture for southern Africa. Significant features of the Cretaceous-Tertiary history of Africa are the following.

1. Africa in the late Cretaceous and Paleocene lay some 15° to the south, well in the region of westerlies, and thus the southern third of the continent probably had a cool wet climate. Relief was low, and a forest flora of the *Podocarpus-Nothofagus* type (not necessarily with *Nothofagus*) is implied for the south, such as occurs today in temperate Australasia and southern South America. Temperate forest existing in the southern Cape today, which is dominated by *Podocarpus*, may be a relict of this flora.

2. By the close of the Cretaceous, Africa was isolated by surrounding ocean, and well separated from South America and India-Madagascar. Direct migration of plants to and from central and southern Africa was limited after the mid-Cretaceous, although indirect interchange with South America was much easier than at present (Raven & Axelrod, 1974). A warm humid climate and low relief probably existed in Africa, except in the cooler south, and consequently a tropical forest flora probably extended over most of the continent. Pockets of aridity are likely even at this time at the edge of the tropics due to high pressure cells and in edaphically dry sites in both tropical and temperate zones (Axelrod, 1972). The small Oligocene fossil assemblage from Banke in Namaqualand, with sclerophyllous characteristics, suggests the evolution of southern sclerophylls from this time, if not earlier, probably on infertile soils.

3. In the later Oligocene the pattern of low relief in Africa (King, 1967) was broken as uplift, especially along the east coast, took place and the present landscape of the continent began to take shape. Uplift implies the formation of cooler and drier belts, especially in the south but also in the tropics.

4. At the same time Australia separated finally from Antarctica which moved south becoming progressively more frigid and a circum-Antarctic circulation was initiated. Progressive drying and cooling effects in the south increased at this time.

5. By mid-Miocene the union of Africa-Arabia with Eurasia was effected, closing the Tethys Sea. Direct migration of the northern Eurasian flora into Africa was possible once again, probably from the Miocene. The newly uplifted highland areas in East Africa became an increasingly significant route for migration to southern Africa.

6. From the Miocene onward, the climate in southern Africa deteriorated. With the continent essentially lying in its present position at the edge of the westerlies, and the influence of cold Antarctic water becoming stronger, aridity would have been increasingly significant. Drought-adapted plants would thus have evolved rapidly from this time.

7. From the late Pliocene onward, important coastal uplift again took place so that the characteristic plateau-escarpment, narrow-coastal-belt landscape of southern Africa was finally formed. Major climatic fluctuations, coinciding with glacial and interglacial periods, resulted in massive migrations of the flora. Changes in climate and of flora are well documented (Martin, 1968; Schalke, 1973; van Zinderen Bakker, 1974, 1978). The Cape Flora, recognizable from pollen samples, is known to have extended to the north at times while the temperate forest covered large areas which are now sclerophyll (Schalke, 1973; van Zinderen Bakker, 1978). A scenario for this period is described in detail by van Zinderen Bakker (1974). These climatic fluctuations must have been responsible for extinction on a large scale and resulted in the restriction of the more mesophytic taxa to favorable sites, hence the number of relicts confined to the coastal and mountain belts from the Cape to Natal. These climatic fluctuations probably were also the cause of the tremendous bursts of speciation in some genera of the Cape and adjacent arid belts as Levyns (1954), Taylor (1978), and others have envisaged. Elimination of some taxa would give opportunities for the evolution of the remaining species into vacant or newly created niches, while the fragmentation of large populations into smaller local ones would promote divergence by genetic drift and rigorous selection in harsher conditions. With amelioration of the climate, changes would favor some taxa more than others, their populations would grow, hybridize with related taxa, and variation and speciation would continue to expand.

RELATIONSHIPS OF THE SOUTHERN AFRICAN FLORA

COSMOPOLITAN, PANTROPICAL, AND PALEOTROPICAL FAMILIES AND GENERA

Of the 200 families of seed plants in southern Africa the majority, some 152, are either more or less cosmopolitan or pantropical (Table 9). A few are represented in the flora by a single species, occurring only in the extreme northern parts, e.g., Opiliaceae, Gyrocarpaceae, Aristolochiaceae, and Cabombaceae. Cactaceae, basically New World, is widespread only by virtue of the easily dispersed *Rhipsalis*, only one or a few species of which occur in Africa and tropical Asia. A few of these widespread families, notably Aizoaceae and Crassulaceae,

TABLE 9. Relationships of southern African phanerogamic families.

Cosmopolitan/Pantropic (not necessarily including Australasia)	152	(Including Aizoaceae; Cactaceae)
Paleotropic (including Australasia)	5	Flagellariaceae, Pittosporaceae (Balsaminaceae, Dipterocarpaceae, Musaceae)
African-Madagascan	6	Hydrostachyaceae, Montiniaceae, Myrothamnaceae, Ptaeroxylaceae, Selaginaceae, Sphenocleaceae (Androstachyaceae, if recognized)
African	4	Melianthaceae, Oliniaceae, Welwitschiaceae (and if recognized, Curtisiaceae, Heteropyxidaceae, Kirkiaceae, Wellstediaceae)
African-Eurasian	10	Balanitaceae, Dipsacaceae, Moringaceae, Neuradaceae, Pedaliaceae, Resedaceae, Salvadoraceae, Tamariacaceae, Trapaceae, Vahliaceae
African-New World	7	Canellaceae, Hydrophyllaceae, Hydnoraceae, Loasaceae, Tecophilaeaceae, Turneraceae, Velloziaceae
African-Australian (and South America)	7	Aponogetonaceae, Cunoniaceae, Escaloniaceae, Haemodoraceae, Podocarpaceae, Proteaceae, Restionaceae (possibly Monimiaceae, Gunneraceae, and if recognized, also Philesiaceae)
Endemic	10	Table 2

can be said to have their center in southern Africa, and several others have undergone particularly extensive radiation here. Among the latter are Compositae—Inuleae, Arctoteae and Calenduleae; Iridaceae; Liliaceae—Aloineae; Ericaceae—Ericoideae; Thymelaeaceae—Thymelaeeae; Rutaceae—Diosmeae; Asclepiadaceae; Geraniaceae; Scrophulariaceae; Oxalidaceae; Zygophyllaceae. The region is also perhaps the center for Hypoxidaceae and Amaryllidaceae—Amaryllideae.

Five families in southern Africa can be said to be Paleotropical (Table 9). Dipterocarpaceae[5] (barely represented here, with one record in northern Botswana); Ptitosporaceae (mainly Australasian with *Pittosporum* in forests of Asia, Africa, and Madagascar); and Flagellariaceae. Balsaminaceae, poorly represented in southern Africa, falls in this group, although it also has minor representation in North America. Perhaps Musaceae (here including Strelitziaceae) also belongs here, although the monotypic *Phenakospermum*, related to *Ravenala*, occurs in the Neotropics. (Balanitaceae, Pedaliaceae, Vahliaceae, and Salvadoraceae are treated in the following pages as Afro-Eurasian families.)

At generic level, the cosmopolitan or pantropical element comprises 22.8% of the flora, or about 425 genera (Table 10). This includes many aquatics, marine and fresh water, as well as some tropical groups rather poorly represented in southern Africa and the large worldwide genera like *Senecio*, *Euphor-*

[5] A monotypic subfamily of Dipterocarpaceae has recently been described (by Maguire et al., 1977) from South America.

TABLE 10. Relationships of southern African phanerogamic genera.

Cosmopolitan/Pantropic (not necessarily including Australasian)	423	(22.8%)
Paleotropic (including Australasian)	255	(13.7%)
African-Madagascan	116	(6.2%)
African	357	(19.1%)
African-Eurasian	78	(4.2%)
African-New World	48	(2.5%)
African-Australian (and South America)	23	(1.2%)
Endemic	560	(30.2%)
TOTAL	1,860	

bia, *Eragrostis*, and *Chenopodium*. Strictly Paleotropic genera (not always in Australia) number 255, 13.7% of all genera in southern Africa.

TROPICAL AFRICAN AND AFRICAN-MADAGASCAN FAMILIES AND GENERA

The southern (-tropical) Africa-Madagascan element (Table 10) is significant with Selaginaceae (essentially southern African and only a few species also in tropical Africa and Madagascar); Ptaeroxylaceae, ditypic, with *Ptaeroxylon* in south tropical Africa, *Cedrelopsis* in Madagascar; Hydrostachyaceae; Myrothamnaceae; and Montiniaceae with *Montinia* in the Cape to southern Angola and *Grevea* in tropical Africa and Madagascar (Milne-Redhead, 1955; Letouzey, 1977). Sphenocleaceae may belong here, but it may better be regarded as a Paleotropical family. If recognized as separate from Euphorbiaceae, Andrastachyaceae must be added to this group.

Some 114 genera of the southern African flora occur in tropical Africa and Madagascar. Essentially tropical groups predominate here but also included are *Aristea* (Iridaceae), *Hebenstreitia* (Selaginaceae), and *Philippia* (Ericaceae), typical Cape-Afromontane taxa, and *Kniphofia* (Liliaceae). Only two genera, *Ernestimeyera* (= *Alberta*: Rubiaceae) and *Protorhus* (Anacardiaceae) are restricted to Madagascar and southern Africa. The species of *Geissorhiza*, confined to the Cape Region, that have been described from Madagascar, are misplaced in this genus and perhaps belong to *Gladiolus*.

Strictly tropical and southern African families are few, including only Oliniaceae (Myrtales), Melianthaceae (Sapindales?) and Welwitschiaceae, the peculiar relict gymnosperm of the Namibia-Angola coastal desert. If accorded recognition, Curtisiaceae (mentioned already), Kirkiaceae (Simaroubaceae here), and Wellstediaceae (Boraginaceae here) could be added to this list. The latter has one species in western southern Africa and one in northeast Africa and Socotra. *Heteropyxis*, frequently assigned its own family, seems best placed in Myrtaceae (Johnson & Briggs, 1978).

A large group of about 360 genera occurs only in tropical and southern Africa (Appendix 3). Some 50 at least are essentially endemic to the subcontinent with minor extensions in south tropical Africa. Many genera belong to the reverse class, predominantly tropical African, and barely represented in southern Africa. Among the latter, the following are some tropical African genera that extend only into northern Namibia, the Caprivi Strip, northeast Botswana or

extreme northern Transvaal: *Amblygonocarpus*, *Brachystegia*, *Guibourtia*, *Julbernardia*, *Baikiaea* (all Leguminosae); *Byrsocarpus* (Connaraceae); *Leiothylax* (Podostemaceae); *Pleiotaxis* (Compositae); and *Oenostachys* (Iridaceae).

There appear to be three significant distribution patterns among the genera of southern and tropical Africa. The majority are tropical taxa, more or less widespread in tropical or south-tropical Africa with their southern limit in the warmer parts of southern Africa. A second group are arid elements of the Karoo-Namib and Kalahari which are absent or have poor representation in the tropics but occur also in northeast Africa. Many arid taxa with distributions of this type extend to the Middle East and northwest India and sometimes to arid southwest Madagascar and are discussed more fully in the section that follows. Examples of strictly African genera with this distribution are *Kissenia* (Loasaceae), *Babiana* (Iridaceae), and *Wellstedia* (Boraginaceae) (Table 11). *Parkinsonia* (Leguminosae) and *Thamnosma* (Rutaceae) have this range in Africa, but also occur in arid areas in the New World (Table 12).

A third group comprises temperate southern African genera, mostly centered in the Cape, which extend outside southern Africa mainly in highland areas, a Cape-Afromontane group (Table 11) (Weimarck, 1941: 90–97). Some genera with this distribution extend well into Eurasia also, such as *Gladiolus* and *Romulea* (Iridaceae) or barely reach the Mediterranean, like *Osteospermum* (Compositae).

AFRICAN-EURASIAN TAXA

While the number of strictly African families is small, there is a substantial Afro-Middle Eastern or African-European-Western Asian representation at the family level, predominantly of xeric groups (Table 10). In the first category are Vahliaceae, and the following, disjunct between southern Africa and northeast Africa: Neuradaceae, Moringaceae (also Madagascar), and Resedaceae.[6] Balanitaceae and Salvadoraceae, though with minor extensions to Burma and the Philippines respectively, belong here, as does Pedaliaceae.[7] More widespread, and in Europe and temperate Asia as well, are Tamaricaceae, Trapaceae, and Dipsacaceae, the latter a temperate family found only in montane regions in the tropics.

Conspicuous south-north distributions at subfamily level are Iridaceae—Ixioideae, very clearly centered in southern Africa, and Ericaceae—Ericoideae (and *Erica* itself) which is very diversified in southern Africa, especially in the Cape Region where 23 genera (19 endemic) and 765 species (753 endemic) occur. Although Ericaceae appears a basically north temperate family (Levyns, 1964), the representation of Ericoideae in Africa may be very old (Raven & Axelrod, 1974) with Ericaceae having originated in west Gondwanaland. Ericoideae in Europe may only date from the Oligocene when migration between Africa and Eurasia was facilitated as these landmasses moved closer, and at the same time coastal uplift in Africa made temperate habitats available in tropical Africa for

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[6] The single species of Resedaceae, *Oligomeris linifolia*, in southwest North America may be recently introduced there (Raven, 1971).

[7] The record of one species, *Rogeria brasiliensis* = *Pterodiscus gayii*, in Brazil appears erroneous (Decaisne, 1865), having arisen due to confusion over an early Angolan collection.

TABLE 11. Some genera of southern Africa with north-south distributions, having limited ranges in Africa or extending into Eurasia, sometimes absent from tropical Africa.

1. Southern Africa-northeastern Africa (including southwestern Arabia)

Angkalanthus
Babiana
Cotyledon
Echidnopsis
Erythrophysa
Kissenia
Macowania
Sesamothamnus
Tetrapogon
Tribulocarpus
Wellstedia

2. Southern Africa-north Africa, Mediterranean and Eurasia

(Centered in s. Africa)
Aizoon
Asthenatherum
Citrullus
Hertia
Gynandriris
Ifloga
Lasiopogon
Lasiospermum
Leyssera
Rogeria
Schismus
Stipagrostis

(Centered in Eurasia)
Ajuga
Andrachne
Ballota
Bartsia
Bupleurum (also North America)
Capnophyllum
Chenolea
Conium
Corallocarpus
Dactyliandra
Dyerophytum
Emex
Erodium
Forskaolea
Geum
Halopeplis
Kochia
Laurentia
Mathiola
Matricaria
Moringa
Oligomeris
Papaver
Seetzenia
Tamarix
Torilis
Trigonella
Valerianella

3. Southern Africa-African mountains (-southwestern Arabia) decreasing northwards (a few also occur in Madagascar)

(Centered in Cape Region)
Aristea
Cliffortia
Disa
Euryops
Felicia
Ficinia
Hesperantha
Moraea
Muraltia
Passerina
Pentaschistis
Phylica
Philippia
Protea
Restio
Ursinia
Stoebe
Struthiola

(Centered in eastern s. Africa)
Alepidia
Anomatheca
Dierama
Dietes
Kniphofia
Knowltonia
Merxmuellera

(Widespread in s. Africa)
Albuca
Athanasia
Berkheya
Cyphia
Cyrtanthus
Delosperma

4. Southern Africa-Africa (mainly montane) -Eurasia (or north temperate)

(Centered in Cape Region)
Erica
Gladiolus
Osteospermum
Pelargonium (-Australia)
Romulea

(Centered in s. Africa)
Androcymbium
Argyrolobium
Helichrysum (-Australia)
Lotononis

(Centered in Eurasia)
Astragalus
Anemone
Cephalaria
Dianthus
Lepidium
Scabiosa
Thalictrum
Valeriana

the first time since the Cretaceous. There are relatively few Ericoideae on the African mountains (*Erica*, *Blaeria*, *Philippia*) and the Madagascar highlands (*Philippia* only). Iridaceae—Ixioideae extend from the Cape through tropical Africa to Europe and western Asia, and *Gladiolus* covers this whole range, other genera being more restricted.

TABLE 12. New World-African (-Madagascan) genera also in southern Africa.

1. Tropical Forest and Savanna

Annona (Annonaceae)
Anthephora (Gramineae)
Asclepias (Asclepiadaceae)
Ascolepis (Cyperaceae)
Aspilia (Compositae)
Caperonia (Euphorbiaceae)
Cienfugosia (Malvaceae)
Ctenium (Gramineae)
Duvernoia (Acanthaceae)
Eriochrysis (Gramineae)
Eustachys (Gramineae)
Guibourtia (Leguminosae)
Hilleria (Phytolaccaceae)
Hyperthelia (Gramineae)
Hyptis (Labiatae)
Kosteletzskya (Malvaceae)
Lippia (Verbenaceae)
Loudetia (Gramineae)
Maprounea (Euphorbiaceae)
Mitracarpum (Rubiaceae)
Newtonia (Leguminosae)
Ocotea (Lauraceae)
Olyra (Gramineae)
Paratheria (Gramineae)
Pentodon (Rubiaceae)
Piriqueta (Turneraceae)
Raphia (Palmae)
Rhipsalis (Cactaceae, also Asia)
Rhytachne (Gramineae)
Sclerocarpus (Compositae)
Siphonoglossa (Acanthaceae)
Sorghastrum (Gramineae)
Swartzia (Leguminosae)
Syngonanthus (Eriocaulaceae)
Tapura (Dichapetalaceae)
Trachypogon (Gramineae)
Trichoneura (Gramineae)
Willkomia (Gramineae)

2. Aquatic

Eichhornia (Pontederiaceae)
Genlisea (Lentibulariaceae)
Heteranthera (Pontederiaceae)
Wolffiella (Lemnaceae)
Wolffiopsis (Lemnaceae)

3. Predominantly Arid Zones

Fagonia (Zygophyllaceae, also Eurasia)
Haematoxylum (Leguminosae)
Hoffmanseggia (Leguminosae)
Menodora (Oleaceae)
Nicotiana (Solanaceae, also Australia)
Parkinsonia (Leguminosae)
Thamnosma (Rutaceae)
Turnera (Turneraceae)

At generic level, there is a substantial arid southern Africa–Middle East distribution pattern, noted above in a few families (Table 11). This usually involves the dry Horn of Africa and as far east as northwest India (Verdcourt, 1969; de Winter, 1971; van Zinderen Bakker, 1975) and often the Mediterranean basin. Dealt with extensively by de Winter (1971) for all taxonomic levels, notable examples are *Tetrapogon*, *Schismus*, *Stipagrostis* (Gramineae); *Moringa* (Moringaceae) and *Cytinus* (Rafflesiaceae), both also in Madagascar; *Seetzenia* and *Fagonia* (Zygophyllaceae), the latter also in America; *Forskaolea* (Urticaceae); *Tamarix* (Tamaricaceae); *Dyerophytum* (Plumbainaceae); *Gynandriris* (Iridaceae); *Emex* (Polyonaceae); *Oligomeris* (Resedaceae—occurring also in North America; it may be introduced there according to Raven [1971]) (Table 11).

Not involving particularly xeromorphic groups are *Papaver* with one species widespread in eastern South Africa, otherwise in the Northern Hemisphere; *Orobanche* (Orobanchaceae), with one or two species native in southern South Africa; *Ifloga*, *Lasiopogon*, *Leyssera*, and *Lasiospermum* (Compositae), predomi-

nantly of the Cape Region with a single species of each genus north of the Sahara. Other examples (Table 11) include *Myosurus* (Ranunculaceae), also in Australia; *Valerianella* (Valerianaceae) with one species endemic in the Cape Region; *Gladiolus* and *Romulea* (Iridaceae), centered in the Cape but extending through the African highlands to Eurasia; *Matthiola* (Cruciferae), Eurasian with one species in South Africa; *Laurentia* (Campanulaceae), Mediterranean and Cape (American species of *Laurentia* are now placed elsewhere); and *Scabiosa* and *Cephalaria* (Dipsacaceae), centered in Eurasia, but with a few species in the African highlands and several in southern Africa.

NEW WORLD-AFRICAN (-MADAGASCAN) FAMILIES AND GENERA ALSO IN SOUTHERN AFRICA

African-New World distributions, unlike the foregoing, are rather unusual, but for southern Africa involve as many as seven families (Table 9) and many more genera (Table 12). This pattern has been reviewed extensively by Thorne (1972). At the family level are the following examples. In Loasaceae, only the genus *Kissenia* is African and disjunct with one species in the southwest and one in the northeast and also in neighboring southern Arabia. Hydrophyllaceae is predominantly North American (see Raven & Axelrod, 1978 for survey of family), but with *Hydrolea* widespread in the tropics. *Codon*, endemic in southern Africa, is the only exclusively Old World genus of this family. Tecophilaeaceae is predominantly southern in distribution, both in Africa and in South America, but with the monotypic *Odontostomum* in California. Velloziaceae, Hydnoraceae, and Canellaceae, all also in Madagascar and the Neotropics, have no genera common to the New and Old World and are about equally represented on both sides of the Atlantic. Their distribution patterns may well have resulted from relatively ancient disjunctions (Raven & Axelrod, 1974: 607–609). Lastly, Turneraceae, which has seven genera, appears more diversified in Africa, with the two New World genera, *Turnera* and *Piriqueta*, also in Africa. In the case of *Turnera*, the one species in Africa is restricted to Namibia, and the remaining 59 in America.

There are some 111 genera restricted to America and Africa (including Madagascar) as estimated by Thorne (1972) but fewer, an estimated 48 occur in southern Africa. Most appear to belong to easily dispersed groups including for southern Africa, some 12 genera of Gramineae, almost all of tropical savannas, two genera of Compositae, three Leguminosae and two Rubiaceae, also of similar habitats (Table 12). Among aquatics are two genera of Lemnaceae (*Wolffiopsis* and *Wolffiella*); *Genlisea* (Lentibulariaceae); and *Eichhornia* and *Heteranthera* (Pontederiaceae). These two broad groupings involve tropical Africa primarily, with these genera poorly distributed in southern Africa.

Among the more interesting disjuncts are a group of xeromorphic taxa found in arid southwestern Africa and in America. These include *Menodora* (Oleaceae; southwestern Africa, South America and Mexico-southwestern U.S.), *Thamnosma* (Rutaceae; southwestern Africa, northeast tropical Africa and North America), *Nicotiana* (Solanaceae; one species in Namibia, otherwise widespread in America and also in Australia); the Caesalpinioid legumes *Hoffmanseggia*

(south tropical Africa and America), *Parkinsonia* (southwestern and northeastern Africa and tropical America), and *Haematoxylum* (southwestern Africa, Mexico and West Indies); and *Turnera* (Turneraceae), one species of which is endemic in Namibia, the remaining widespread in America.

Most New World-African (-Madagascan) disjunct genera are likely to have achieved this distribution in fairly recent times by long distance dispersal. This would probably have been easiest during the more extreme arid phases of the later Tertiary for the distinctly arid elements. More direct migration would seem unlikely except for the few sufficiently ancient to have been in existence in the Paleogene when Africa and South America were substantially closer (Axelrod & Raven, 1978), with numerous islands in the then shallower Atlantic leaving much smaller water gaps.

Some of the disjunct families, especially those with good representation on both sides of the Atlantic, were probably in existence in the early Tertiary when the Atlantic was much narrower and short distance migration was thus possible. Velloziaceae, Tecophilaeaceae, Turneraceae, Hydnoraceae, and Canellaceae, having differentiated by late Cretaceous in West Gondwanaland, could perhaps have migrated more or less directly or by island hopping into the early Eocene. The only non-American genus of Loasaceae, *Kissenia*, might also have some antiquity in Africa (Raven & Axelrod, 1974).

AUSTRAL TAXA

Families, Subfamilies, and Tribes.—Relatively few taxa are restricted to all of the southern continents (some widespread weeds excepted), and these are mainly at family or subfamily level (Tables 10, 13). These, or elements common only to southern Africa and Australasia, have been the subject of much interest in relation to the Cape Flora (Adamson, 1948, 1958), for most distributions of this type involve the Cape Region more than the rest of southern Africa. Most well known are Proteaceae and Restionaceae and these will be discussed more fully below. Another important example is Cunoniaceae with two genera each with a single species in southern Africa, *Platylophus*, a Cape forest endemic, and *Cunonia*, widespread in the temperate Cape forest and also in sheltered areas in eastern South Africa. *Cunonia* is otherwise restricted to New Caledonia. The most widespread member of Cunoniaceae is the tropical genus *Weinmannia*, occurring in Madagascar and the New World, as well as Asia and Australasia where Cunoniaceae are most diversified.

Haemodoraceae is centered in Australia, but is well represented in the Cape Region by three genera with a fourth, *Barberetta*, in the eastern Cape and Natal. The family also occurs in North and South America. Another monocot alliance, Philesiaceae (Hutchinson, 1959), more usually included in Liliaceae, includes *Behnia* in eastern south and south tropical Africa, and other genera in temperate South America and Australia. To these monocots Liliaceae—Colchicoideae (Wurmbeoideae) can perhaps be added. This subfamily is best developed in southern Africa, with some species in tropical Africa and Madagascar and Eurasia, where the very reduced *Colchicum* (and *Merendera*) and one species of *Androcymbium* occur. *Wurmbea* is disjunct between Africa and Austral-

Table 13. Survey of southern (-tropical) African-Australasian genera.

Aizoaceae		
	Carpobrotus	17 Cape; 5 Australia, also New World
	Disphyma	1 Cape and Australia
	Tetragonia	33 southern Africa; 20 Australasia, also South America
Aponogetonaceae		
	Aponogeton	12 southern and tropical Africa; 8 Australia, tropical Asia, with 2 fossil records from Argentina
Bombacaceae		
	Adansonia	7 Africa and Madagascar; 2 western Australia
Campanulaceae		
	Grammatotheca	1 southern Africa and Australia where it may be introduced
Compositae		
	Athrixia	12 Africa and Madagascar; 8 Australia
	Cotula	Many on all southern continents
	Helipterum	12 Cape; 50 Australia
Cunoniaceae		
	Cunonia	1 Cape; 12 New Caledonia
Cyperaceae		
	Carpha	3 southern Africa; 11 circum-Antarctic
	Costularia	3 Africa and Madagascar; 11 Australia
	Tetraria	45 Africa (mainly Cape); 5 Australasia and Borneo
Gramineae		
	Triraphis	4 tropical and southern Africa; 2 Australia
Iridaceae		
	Dietes	5 Africa; 1 Lord Howe Island
Liliaceae		
	Bulbinella	5 southern Africa; 10 New Zealand
	Caesia	3 South Africa and Madagascar; 5 Australia
	Wurmbea	12 southern and tropical Africa; 12 Australia
Menyanthaceae		
	Villarsia	1 Cape; 1 southeast Asia; 12 Australia
Myrtaceae		
	Metrosideros-Mearnsia	1 Cape; 60 Australasia–Pacific
Podocarpaceae		
	Podocarpus	Many on all southern continents, extending to tropics
Portulacaceae		
	Anacampseros	40 southern Africa; 1 Australia
Rosaceae		
	Acaena	1 Cape and Karoo; 90 circum-Antarctic and California
Sapindaceae		
	Atalaya	3 southern Africa; 6 (Indonesia–) Australia
Urticaceae		
	Australina	6 tropical and southern Africa; 4 Australasia

asia, whereas *Iphigenia* occurs as well in India and Madagascar. Two other prominent liliaceous disjuncts are *Caesia*, in South Africa, Madagascar, and Australia, and *Bulbinella*, which, with several species in and around the Cape Region and also New Zealand, clearly needs investigation.

The native southern African conifers, *Podocarpus* and *Widdringtonia*, are both clearly Austral (Li, 1953) and are an ancient element. Both are represented in the Neogene fossil record, with *Podocarpus* also recorded from pre-Creta-

ceous time. *Widdringtonia*, which extends from the Cape to Malawi (Kerfoot, 1975), belongs to the widespread Cupressaceae. It is placed in the predominantly southern Callitroideae (only *Tetraclinis* in North Africa occurs in the Northern Hemisphere), and *Widdringtonia* is related closely to the Australasian *Libocedrus*, *Diselma*, and *Austrocedrus* (Gaussen, 1968; Florin, 1963). Northern fossils assigned to *Widdringtonia* probably are misplaced according to Florin.

Three other families, Gunneraceae, Escaloniaceae, and Monimiaceae, each with a single species in southern Africa, may also be considered Austral. The latter, represented by the monotypic *Xymalos* in Africa, is well developed in adjacent Madagascar, and the Mascarene Islands and possibly represents an ancient tropical element now reduced to near extinction in tropical Africa, rather than an Austral one. Monimiaceous wood has been identified from the upper Cretaceous of Pondoland (Muller-Stoll & Mädel, 1962). Dyer (1975) places *Xymalos* in Trimeniaceae and this treatment, if correct, would strengthen the Austral character of the genus with the other representatives of this family being *Trimenia* and *Piptocalyx* in Indonesia, New Guinea, and Australia.

In Leguminosae, the distribution of the relatively primitive Podalyrieae in the Cape Region and Australia has often been cited as an example of the affinities of these floras. Polhill (1976) regards the similarities here as convergent, with Australian and Cape "Podalyrieae," derived independently from unspecialized tropical ancestors (Sophoreae).

Australian-South African Genera.—At the generic level several Austral or African-Australian groups stand out, though the number is small, some 25 (Table 13). In Aizoaceae these include *Disphyma* (one species, salt flats or coastal, Cape and Australia), *Carpobrotus* (about 25 species, mostly coastal, Cape and adjacent areas, Chile, Australia, and California), and *Tetragonia* (about 33 species, desert or coastal in southern Africa, coastal in western South America and Australasia). All seem relatively easily dispersed (Raven, 1973; Seavey & Raven, 1977) and not ancient links between southern land masses.

Among the inuloid Compositae, *Helipterum* (Cape and Australia) and *Athrixia* (Africa, Madagascar, and Australia) are disjunct, although there is some question as to whether Australian representatives are actually congeneric with the African ones (Bentham, 1873: 423). The one species of the Australian *Cassinia* in South Africa is now regarded as belonging to a different though closely related genus, *Rhynea* (Hilliard, 1977). Inuleae are well developed in Australia and in Africa, in the south particularly, but *Gnaphalium* is very widespread, and *Helichrysum*, also well represented in Madagascar, occurs in Eurasia, southern India, Ceylon, and Australia. The group is evidently easily distributed and the connection is probably via Asia.

In Bombacaceae the range of *Adansonia* (9 species) has received much attention with the one or two species in Western Australia apparently closely related to some in Madagascar (Perrier de la Bâthie & Hochreutiner, 1955). Long distance dispersal appears the most likely explanation for this distribution (Raven & Axelrod, 1974). *Dietes* (Iridaceae) is a similar case with five species in east tropical and southern Africa and one, undoubtedly related, on Lord Howe Island between Australia and New Zealand. *Dietes* probably achieved this dis-

tribution through long distance dispersal, although it is not possible to say when and how. *Dietes*, being one of the more primitive African genera of the family, might be of Paleogene origin. The distribution of *Villarsia* (Menyanthaceae) is as remarkable as *Dietes*: there are 12 species in Australia, one in southeast Asia and one in the Cape Region. The Cape *Villarsia capensis* is heterostylous and strongly self-incompatible (Ornduff, 1974) and is related to eastern Australian species rather than to those in western Australia. The distribution of *Atalaya* (Sapindaceae), with three species in southern Africa and six in Indonesia and Australia, probably is another example of long distance dispersal, perhaps in mid-Tertiary times. The occurrence of a single distinctive species of *Mearnsia* ("*Metrosideros angustifolia*") (Myrtaceae; Dawson, 1975) in the Cape Region, the rest of the complex being Australasian and Pacific, may have dispersed around the Indian Ocean like *Adansonia*, but in reverse direction (Raven & Axelrod, 1974).

In Rosaceae, *Acaena*, essentially circum-Antarctic, but in the New World also to California and Hawaii, has only a single species in the Cape Region and nearby mountains and is easily dispersed by birds. The widespread *Cotula* (Compositae) is concentrated in the southern continents. Like *Acaena*, it is probably readily dispersed.

In Cyperaceae, *Carpha* is circum-Antarctic, *Costularia* occurs in Africa, Madagascar, and Australia, and *Tetraria* is found predominantly in the Cape and in Australia. Gramineae—Danthonieae also seems primarily Austral and is particularly well represented in temperate South Africa. If taken in its wide sense, *Danthonia* is a disjunct Austral genus with very minor representation north of the equator, but the African species have been segregated in several genera—*Karoochloa*, *Merxmuellera*, *Dregeochloa*—all of more restricted range. The Austral connection remains, however, at the tribal level.

The predominantly southern distribution of Proteaceae is well known, with the family centered in the Australasian region, but with significant representation in South America and in Africa, where in both areas concentration decreases towards the equator. The phytogeography of the family has recently been critically surveyed (Johnson & Briggs, 1975, 1978). In Africa and Madagascar, only two subfamilies, Grevilleoideae and Proteoideae, of five now admitted by Johnson & Briggs (1975) occur, and only the latter, Proteoideae, are well represented. The family is best developed in the south and 12 of the 13 African genera occur in the Cape Region, where 10 are endemic, including the only strictly African grevilleoid genus, *Brabeium*. The remaining genus *Faurea*, also in Cape temperate forest, is widespread in tropical Africa, and also occurs in Madagascar. Only *Protea* and *Faurea* are well represented in tropical Africa, and *Faurea*, with an elongated inflorescence and forest savanna habitat, appears primitive in the subfamily. Although *Faurea* itself is not likely to have been the direct ancestor of the remaining proteoid genera (Johnson & Briggs, 1963, 1975) a more generalized ancestral form could well have been. African Proteoideae may thus have had an origin from tropical African forest ancestors of the *Faurea* type.

Grevilleoideae, an essentially tropical group (Johnson & Briggs, 1975) has

one genus, *Brabeium*, in the Cape and one, *Malagasia*, in Madagascar. Elsewhere the subfamily occurs in tropical Australasia and in South America. *Brabeium* appears significantly southern until the basically tropical nature of Grevillioideae is recognized, and it seems most likely to be the only surviving representative of a subfamily now extinct in tropical Africa. The existence of *Malagasia*, a monotypic genus of the subfamily in Madagascar, appears to reinforce this point of view. With these facts in mind, I have no difficulty in supporting a tropical African origin for southern African Proteaceae (Levyns, 1958; Beard, 1959; Johnson & Briggs, 1963, 1975; Raven & Axelrod, 1974), and a tropical origin for the family as a whole, as argued by Johnson & Briggs (1963, 1975). This would imply Late Cretaceous dispersal over some water gaps in the subtropical region now occupied by the Indian Ocean (Raven & Axelrod, 1974).

Restionaceae, the other major so-called southern element in the southern African flora, has a distribution similar to that of Proteaceae, although it is represented in South America only by one genus, which is common to Australia. Restionaceae is more diverse anatomically and palynologically in Australasia (Cutler, 1972; Johnson & Briggs, 1978; Ladd, 1977), but there are more species in Africa where the family is almost entirely confined to the Cape and adjacent areas. Only two species, both of *Restio*, the least specialized of the African genera, occur outside South Africa itself, one in Malawi and one in Madagascar. Contrary to some current views, Australasia and Africa share no genera, and the groups found on the two continents are not closely related (Gilg-Benedict, 1930; Johnson & Briggs, 1975, 1978; Cutler, 1969). Reports of Restionaceae pollen from the Eocene of Europe (see Chandler, 1964, for survey) are remarkable if correct (Levyns, 1964; Raven & Axelrod, 1974), and as Johnson & Briggs (1978) suggest, may well represent extinct unrelated or distantly allied monocotyledonous groups. Restionaceae has minor extensions in tropical Asia to Indochina, but seems basically southern, more so than Proteaceae. With more limited fundamental variation in Africa at higher taxonomic levels, Restionaceae may have reached here from Australia by dispersal across a narrow Indian Ocean in the Late Cretaceous. This may best account for its very southern distribution pattern in Africa as suggested by Raven & Axelrod (1974) and Cutler (1972).

Summarizing Austral distribution patterns, there are relatively few genera common to Australasia (and South America) and southern Africa (Adamson, 1958), and these probably achieved this distribution by long distance dispersal. Several seem easily distributed—*Acaena*, *Carpobrotus*, *Tetragonia*, *Costularia*, *Cotula*—while others like *Adansonia*, *Dietes*, *Villarsia*, and *Mearnsia* are so disproportionately represented in one or the other area, that long distance dispersal seems again likely, however difficult this may be to envisage.

At the family level Proteaceae seems basically tropical, and the richness in southern Africa is likely to have evolved from tropical African ancestors rather than from any direct Austral migration. Restionaceae and Cunoniaceae in southern Africa may have been derived from tropical African ancestors now extinct there, but perhaps reached south tropical Africa early in the Paleogene by dispersal across a narrower Indian Ocean. Direct Austral links with the southern

African flora are in fact probably limited to the gymnosperms *Podocarpus* and *Widdringtonia* with other groups having had a history in Africa as a whole (Proteaceae) or having reached south or south tropical Africa early from Australasia.

ORIGINS OF THE FLORA

Simplifying the patterns discussed, it is clear that a large proportion of the southern African flora is part of a cosmopolitan or pantropical flora, including for example Rubiaceae, Gramineae, Leguminosae—Caesalpinioideae, and Cucurbitaceae, groups in which the endemic element is small. Such groups are particularly well represented in the Kalahari-Highveld Region, and become dominant in the Zambezian flora in the northern part of southern Africa. Evolution from tropical African forest and savanna elements for most of the constituents of these regions is suggested, with some taxa arriving from the Asian and New World tropics by long distance dispersal or from Asia by more or less direct migration before the formation of deserts in North Africa and Eurasia.

The arid Karoo-Namib flora received some of its peculiar elements by short distance dispersal or by direct migration from arid Eurasia via Somalia-Kenya (with the reverse also taking place), and conditions for this were probably best when arid phases of the Pleistocene were at a maximum and distances between arid zones least (Verdcourt, 1969; Raven, 1972; van Zinderen Bakker, 1975; Werger, 1978b), or possibly when a continuous arid belt existed across Africa. A few taxa may have reached here directly by long distance dispersal (Axelrod & Raven, 1978) from South America, e.g., *Nicotiana*, *Turnera*, *Menodora*, *Haematoxylum*, also during arid phases of the latest Tertiary and Quaternary. The highly endemic nature of this specialized desert flora, however, suggests that much of it has evolved in southern Africa over a very long period. There has always been a zone of reduced precipitation between tropical and temperate regions, as well as edaphically dry habitats (Axelrod, 1972), where drought adapted plants existed. The present Karoo-Namib flora would thus be derived in part from an ancient xeric stock in which evolution and radiation were promoted from the Neogene as the African climate became progressively drier.

Additions to this ancient stock probably occurred continuously from tropical African elements to the north (Bews, 1925; Levyns, 1964) and from an old temperate southern African flora (Compton, 1929). Woody taxa in the Karoo-Namib have tropical affinities, e.g., *Rhigozum* (Bignoniaceae); *Erythrophysa* (Sapindaceae); *Commiphora* (Burseraceae); *Nymania* (Meliaceae); *Euclea* (Ebenaceae). The relationship between the Cape and Karoo floras has often been noted (Bolus, 1905; Acocks, 1953: 5), and many Compositae, Scrophulariaceae, and Selaginaceae important in the Karoo seem most closely related to Cape rather than to tropical taxa, as is the case with *Oxalis* (Oxalidaceae), *Babiana* and *Gladiolus* (Iridaceae), *Pelargonium* (Geraniaceae), and other herbaceous forms. Relict patches of Cape Flora in favorable sites are characteristic in Namaqualand and the southern Karoo, though the two floras do not appear to merge to any extent (Levyns, 1964).

The Tongaland-Pondoland coastal forest is clearly related to the East African coastal tropical forest, and secondarily to the Guinea-Congolean tropical rain forest. The region is reviewed in detail by Moll & White (1978). It is much restricted now to the most mesic sites in southern Africa and was presumably more widespread in warmer and moister phases of the later Tertiary and Quaternary and ultimately continuous with an earlier, widespread tropical African forest. *Rhynchocalyx* (Lythraceae or Crypteroniaceae (van Beusekom-Osinga & van Beusekom, 1975)) and the cocosoid palm *Jubaeopsis* are conspicuous relicts here.

The Afromontane regions of southern Africa have some taxa in common with similar floras in tropical Africa, such as *Helichrysum* (Compositae), *Craterocapsa* (Campanulaceae), *Kniphofia* (Liliaceae), and *Dierama* (Iridaceae). Its links to the Cape Flora seem much closer, many typical Cape genera extending to the Drakensberg, for example, *Watsonia* (Iridaceae), *Erica* and *Philippia* (Ericaceae), *Cliffortia* (Rosaceae), *Muraltia* (Polygalaceae), and *Aspalathus* (Leguminosae). The contribution of Cape taxa to the Afromontane zones decreases towards the equator, and northern temperate elements become more common, e.g., *Juniperus* (Cupressaceae), *Sedum* (Crassulaceae), *Carduus* (Compositae), *Delphinium* (Ranunculaceae) (Hedberg, 1965). North temperate taxa in the southern African-Afromontane flora are few, including Dipsacaceae, *Lepidium* (Cruciferae), *Thalictrum* (Ranunculaceae), *Vaccinium* (Ericaceae), and *Festuca* and *Koeleria* (Gramineae).

The origin of the Cape Flora, the most distinctive in Africa, presents the greatest problem. As discussed, the so-called Austral or temperate southern element suggestive of ancient links with other southern lands is relatively small. Some of them like Proteaceae may have evolved from ancient tropical African rather than from more temperate southern ancestors derived directly from Australia or South America. At present it seems that a true Austral element is restricted to the conifers *Widdringtonia* and *Podocarpus*, which may have been in southern Africa since these groups evolved and possibly some other elements of the Cape temperate forest (?Cunoniaceae). Restionaceae probably arrived in southern Africa in Late Cretaceous or Paleogene time (Axelrod & Raven, 1978), across a narrower Indian Ocean.

Direct contributions from other floras are minor except from the Karoo-Namib, whence a substantial representation of Aizoaceae, and perhaps other succulents derives. Taxa of north temperate origin apart from Ericaceae—Ericoideae, which might equally be an ancient temperate African group, may be *Lobostemon* and *Echiostachys* (Boraginaceae) (Levyns, 1964), related to the northern *Echium*, and the three endemic genera of Papaveraceae—Fumarioideae, a subfamily centered in the Mediterranean and Middle East. There are few other examples (Burtt, 1971; Quézel, this symposium), e.g., the single native Cape species of *Erodium* (Geraniaceae), *Valerianella* (Valerianaceae), *Ballota* (Labiatae), and *Bupleurum* (Umbelliferae). Other northern genera like *Linum*, *Anemone*, *Silene*, *Scabiosa* and *Dianthus* have species in the Cape but occur elsewhere in southern Africa and often in Afromontane areas as well. In Ericaceae, Levyns (1964) suggests that the family migrated from Eurasia, if so, prob-

ably after mid-Oligocene time, via the African highlands to the Cape. The endemic Cape genera which are highly specialized (Oliver, 1977a) could have evolved once Ericaceae reached the Cape on the peculiar, infertile and acidic sandy soils of the region, but the subfamily can equally well be seen as being an ancient southern group, with migration having taken place from the Cape to Eurasia. The massive speciation in the Cape, however, probably occurred from the Pliocene onward.

For the remainder, such typical elements as Rutaceae–Diosmeae and Thymeleaceae probably evolved gradually from tropical ancestors (Bews, 1925). Significantly the most primitive and widespread genus of Diosmeae, *Calodendrum*, is a broad-leafed tree widespread in Africa (Levyns, 1964), while more primitive broad-leafed Thymelaeaceae such as *Octolepis* and *Peddiea* occur in Africa, in forest habitats, but are not found in the Cape. Origin of the Cape Penaeaceae, all sclerophyllous shrubs, from the broad-leafed African family Oliniaceae, suggested by Levyns (1964), or from other African Myrtales may be a parallel example (Mújica & Cutler, 1974; Rao & Dahlgren, 1969).

Iridaceae, a family most diversified and best represented in Africa, could have evolved the peculiar corm-bearing geophytes of the Cape Region and nearby areas from less drought-adapted, forest forms (e.g., *Dietes*) or from evergreen highland genera (e.g., *Dierama*), as climates deteriorated from the Oligocene onwards (Goldblatt, 1976c). This family is not as strongly restricted to the Cape Region as many others, with many genera quite widespread. Quaternary bursts of speciation apparently have resulted in the overwhelming numbers in the Cape Region today. Papilionoideae—Podalyrieae, Liparieae, and Crotalarieae—so well represented in the Cape and with the latter also in tropical Africa, appear to have differentiated in or near the Cape from Sophoreae still occurring there (Polhill, 1976) and may have radiated subsequently in tropical Africa, Eurasia, and elsewhere.

If it is possible to generalize briefly for so large and diverse a flora, it seems that the Cape Flora is a fundamentally African one as Adamson (1958) and Levyns (1964) asserted, having evolved gradually during the Tertiary from two main sources: first, from an ancient temperate southern African flora probably not much younger than the angiosperm group as a whole (Africa was situated 15°S in the Cretaceous, providing a substantial temperate land surface); second, from tropical African elements, possibly via an upland temperate African pathway. Additions from Eurasia either migrating south in Neogene time and, more recently, along the uplifted African highlands or arriving by long distance dispersal are minor by comparison. The small Austral element of recent genera probably reached the Cape by long distance dispersal (e.g., *Villarsia*, *Metrosideros-Mearnsia*, and *Acaena*). In contrast, ancient Austral cool temperate elements are few, such as *Podocarpus* and *Widdringtonia*, which may be relicts of a truly south temperate (*Nothofagus* type) rain forest such as is still found in southern Australasia and South America.

Evolution of this rich and diverse flora, which has few direct relationships, must have been long and complex. Differences between the Cape Flora and

other African floras surely indicate its great antiquity, reflecting the divergent development of temperate and tropical floras, isolated increasingly since the Paleogene by a belt of increasing aridity. The Cape Flora is essentially the temperate flora of the southern end of Africa, but its peculiarities are strongly linked to the unusual infertile soils of the Cape System. The Mediterranean climate that prevails over most of the Cape Region seems to have been of Quaternary origin (Raven, 1973; Axelrod, 1973) and to have affected the flora mainly by stimulating speciation in an already rich and complex area. Conditions of extreme climatic fluctuation and aridity during the Quaternary would appear to have been directly responsible for the extraordinary richness of the southern African flora. This is in marked contrast to the situation in tropical Africa. Dry phases of this period are believed to have caused massive extinction resulting in the very depauperate tropical African flora (Richards, 1973; Raven & Axelrod, 1974) compared with that of the Neotropics and Asia. It would seem that Africa is the "odd man out" not only in its poor tropical flora but in its remarkably rich southern temperate flora.

THE CAPE AS A MEDITERRANEAN FLORA

The distinctive Cape flora is usually defined by its characteristic element, the fynbos, and I have drawn the boundaries of the Cape Floristic Region around the major belts of this vegetation type. The distribution of fynbos however, follows a geological rather than climatic pattern, with most fynbos, and certainly all fynbos in marginal areas, restricted to sandstones of the Cape System. The climate of southwestern Africa is influenced by winter cyclonic rain, but the pattern of winter rainfall (Fig. 5) does not follow, except very generally, the distribution of Cape sandstones, with winter rainfall extending somewhat inland and far to the north of the Cape Region as here defined. Moreover, in the eastern portion of the Cape Region at least half of the precipitation (Adamson, 1938; Coetzee & Werger, 1975) falls in summer months, and this is especially true of the fynbos-clothed Langeberg, Swartberg, and Outeniqua Mountains of the southern Cape. The dry lowlands between these mountains are more dependent on winter rainfall, which is more important here than any summer precipitation.

The correlation between the Cape Floristic Region and Mediterranean climate is thus a loose one, as pointed out by Marloth (1929) and others, and the adaptations of the fynbos are not primarily to the winter rainfall pattern but more likely to peculiar soils under climates of rather irregular but year-round rain. Of course, many species in the Cape flora, whether fynbos or other vegetation, occur in the western half of the Cape Region, where a strictly Mediterranean climate does prevail. There is no difference in the proportion of winter rainfall (over 70%) in the western part of the Cape Region and in the Karoo-Namib Region to its north and east, but the amount of rainfall decreases outside the Cape Region. Local areas of higher rainfall, however, also have relict patches of Cape flora (Marloth, 1929; Adamson, 1958) though not on notably infertile soils, e.g., *Protea* and *Leucospermum*, Restionaceae, and Ericaceae on the upper Ka-

miesberg; *Phylica*, *Cliffortia*, *Lobostemon*, *Muraltia*, and *Erica plukenetii* on the Spektakelberg; and *Muraltia*, *Cliffortia*, Restionaceae, and Iridaceae on the Roggeveld escarpment and Hantamsberg. These islands of vegetation with some elements of Cape flora do not have Cape sandstone soil, and although they do have as much rainfall as occurs in dry parts of the Cape Region, lack true fynbos. Climate in the Karoo-Namib immediately north of the Cape Region can nevertheless reasonably be called Mediterranean in terms of amount and annual distribution of rainfall, receiving as much moisture as the California Central Valley, the Mediterranean flora of northern Baja California, the dry interior of Spain, or the north coasts of Egypt and Libya.

The Cape Flora, clearly a remarkably distinct floristic unit, occurs in a region of predominantly Mediterranean climate, but, with up to 60% summer rain locally, is thus not strictly the flora of Mediterranean southern Africa. In practical terms it is, however, often convenient to consider it as such, since regions of predominantly winter rainfall to the north have less rain (Fig. 5) and a very characteristic semidesert vegetation unrelated to the Cape fynbos. A rigid definition of the flora of Mediterranean South Africa would, however, probably include all of the Cape Region and parts of the northwestern Cape Province (i.e., Namaqualand) depending on the climatic criteria used.

The Cape Region and Namaqualand have all the characteristics of Mediterranean floras as outlined by Raven (1971, 1973). These are first, medium to low precipitation in the cool part of the year, a dry summer, and flowering concentrated in the spring. Second, a vegetation of sclerophyllous shrubs and evergreen trees with a tendency for small, simple leaves. Third, a strong degree of adaptation to fires, seen especially in the development of underground organs and in seed germination after burning. Fourth, a comparatively rich flora with many very local species. Fifth, an uneven radiation of isolated dicot and monocot groups resulting in several conspicuously large genera and a high species to genus ratio. A rich annual flora is characteristic of the California Floristic Province and the Mediterranean, but there are relatively few annuals in the Cape Region, and not many more in the winter rainfall belt to its north. There also appears to be a poor annual flora in the parts of Western Australia with a Mediterranean climate (Raven, pers. comm.), where the sclerophylls are also associated with infertile soils.

The Cape Region, as compared to other areas of Mediterranean climate, stands out as being particularly rich in species and with very high endemism at species and genus level. Raven (1971) suggests about 10% genera and 40% species endemic in the Mediterranean, while 6.5% genera and 47.7% species are endemic in the California Floristic Province (Raven & Axelrod, 1978) as compared with 20.7% genera and 73.1% species endemic in the Cape Region. The Cape Region also stands out as being unusually high in petaloid monocots which comprise some 16% of the total flora, and though the Cape does not have an unusual number of monocots on a world scale, it has proportionately more monocots than California. The Cape Flora also has far more succulent species than other regions of Mediterranean climate.

Reasons for the unusual richness and high endemism in the Cape Flora are

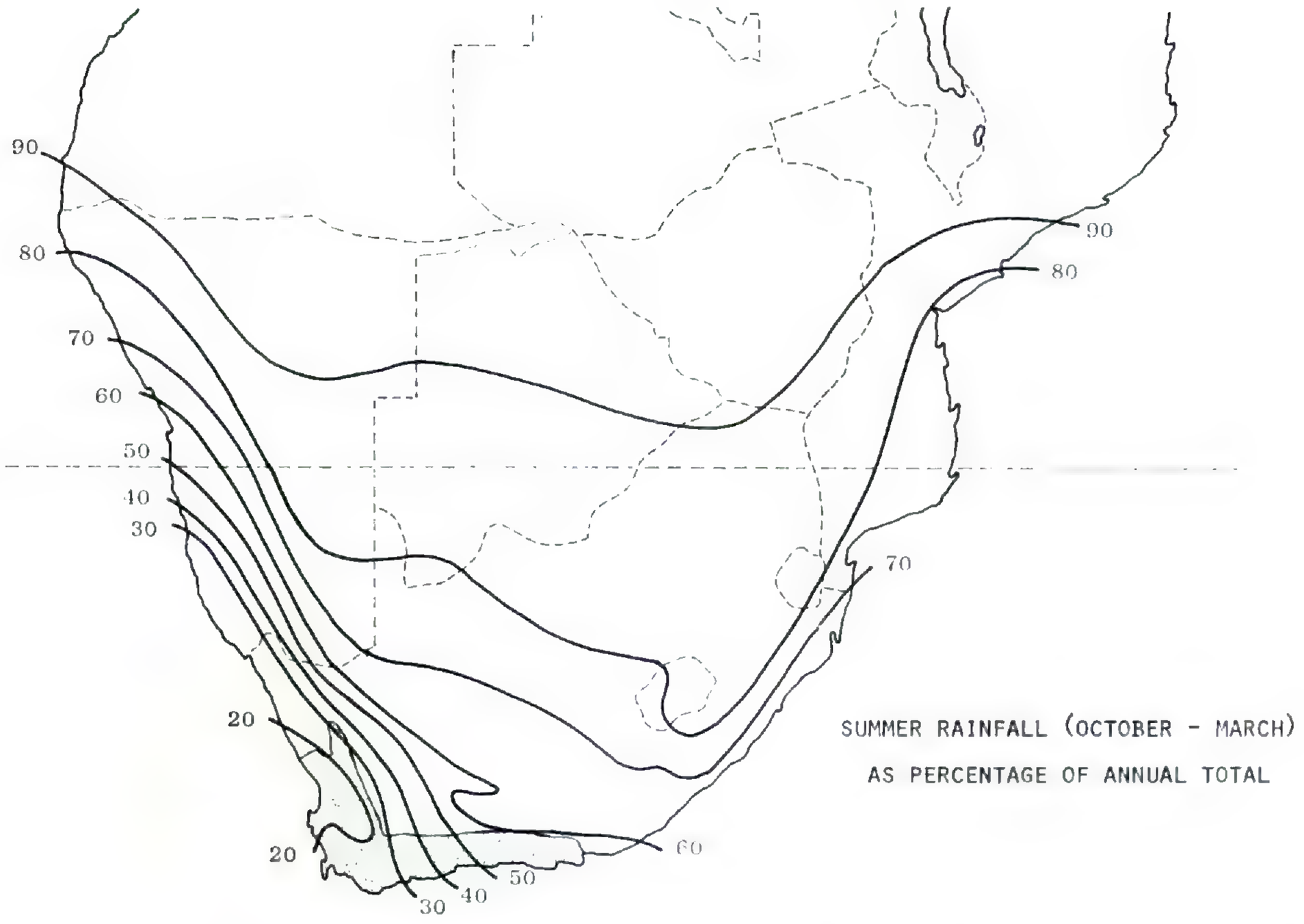

FIGURE 5. Summer rainfall (October–March) as a percentage of the annual total for southern Africa, with the Cape Floristic Region shadowed.

not at all clear. Since climates are comparable in all Mediterranean areas of the world, the explanation must lie elsewhere. It may lie partly in topography and partly in soil. The Cape Region has a very dissected landscape consisting of several steep mountain ranges aligned parallel to the coast and in series behind one another. Each range has appreciable differences in climate and each is isolated from the next by drier flats or valleys, themselves climatically distinct and isolated. This mosaic is reinforced by soil differences, the mountains generally being composed of sandstone rocks and the valleys of shale. There are also large areas of low-lying coastal sands and some limestone.

While this landscape under Mediterranean climatic conditions would obviously promote great species diversity, it is not at all certain that it would account for the far greater numbers of species than are found elsewhere. The topographic and climatic diversity is no more than in California for example. The insect fauna, especially the bee fauna, of the Cape is not particularly rich (Michener, this symposium and pers. comm.), so that a diversity of pollinators does not help in explaining the richness. In fact, the Cape Region is far poorer than California or the Mediterranean in bees, both polylectic and oligolectic. Western Australia, much poorer in species than the Cape (Raven, pers. comm.), has a well-developed series of infertile soils with a characteristic sclerophyllous vegetation that is not confined to regions of Mediterranean climate (Johnson & Briggs, 1978). The topography of Western Australia is much less rugged than in the Cape Region, however, and one might therefore postulate that the unique combination of an equable climate, infertile soils associated with a well-devel-

oped and relatively old (Oligocene ?) sclerophyllous vegetation, a rugged topography, and the multiplying effects of the development of warm season aridity, which by eliminating some kinds of plants allowed others to proliferate extensively, are among the factors responsible for the floristic richness and diversity here.

MODES OF EVOLUTION

There are many books and reviews dealing with plant evolution and speciation in general, but these phenomena have barely been studied in southern Africa. The basic knowledge of the flora is available so the time is ripe for biosystematic and evolutionary research. Though few such investigations have been undertaken, patterns of species distribution and relationships and what is known about hybridization and chromosome cytology do suggest certain trends.

GEOGRAPHIC SPECIATION

Geographic speciation is undoubtedly of primary importance for the southern African flora, especially for areas in the south and west with dry and Mediterranean climates and dissected topography. It would also appear significant in the montane areas of eastern South Africa. This is evident in the recurring pattern in many genera of allopatry or vicarism in closely related species. Levyns (1954) has proposed such a mode of evolution in *Muraltia* (Polygalaceae), and Rourke (1972) envisages geographic speciation in *Leucospermum*. Other Proteaceae appear to exhibit similar patterns of speciation. Bremer (1976a) also draws attention to geographic speciation in his revision of *Relhania* (Compositae), while Strid (1972) mentions examples in *Adenandra* (Rutaceae).

The mode of evolution operating under conditions such as are found in southern Africa (Axelrod, 1967: 203) could account for much of the diversity of species here (Raven, 1964; Axelrod, 1967). Fluctuations in the climate of the world during the late Tertiary and Quaternary had their counterpart in southern Africa where alternating arid and mesic phases occurred (van Zinderen Bakker, 1974, 1978; Schalke, 1973; Tankard & Rogers, 1978). Evolution under circumstances of increasing aridity in areas of moderate to low precipitation promotes geographic isolation (Stebbins, 1952; Raven, 1964) of populations, with consequent differentiation of races, and then species. Geographic speciation, especially in the arid south and west, is likely to have been rapid, and much of the richness at the species level is of recent origin—hence the high species per genus ratios for arid areas of the world and for southern Africa particularly. Uneven evolution of isolated families and genera under these conditions (Stebbins, 1952; Raven, 1972) typically occurs as an accompanying phenomenon.

HYBRID SPECIATION

Speciation at the diploid level through the formation of hybrid complexes—homogamic complexes of Grant (e.g., 1971: 297)—is known to be important in the California flora (Raven & Axelrod, 1978) which is ecologically comparable to the arid and Mediterranean parts of southern Africa. This process is poorly

known in southern Africa, but important in *Streptocarpus* (Gesneriaceae; Hilliard & Burtt, 1971). Many other genera in the flora exhibit features which suggest that hybridization may be significant. Natural hybrids between species of both woody and herbaceous taxa are known notably in *Protea* (Rourke, pers. comm.) and even between genera of Proteaceae (Rourke, 1976), in *Streptocarpus* (Hilliard & Burtt, 1971), *Euryops* (Nordenstam, 1968a), *Erica* (Oliver, 1977b) and in several genera of Iridaceae: e.g., *Babiana*, *Homeria*, and *Gladiolus*. Artificial hybrids are readily produced and often are fertile: e.g., *Zantedeschia* (Araceae; Horn, 1962) and in *Sparaxis*, *Ixia*, *Watsonia*, *Gladiolus* (Iridaceae; Horn, 1962; T. T. Barnard, pers. comm.) but not always so. In two other genera of Iridaceae, *Romulea* and *Moraea*, intersectional hybrids cannot be produced (de Vos, 1972, Goldblatt, unpubl. data) and even within sections only closely related species seem to hybridize easily. Hybrids are also particularly well known in *Rhus* and in *Aloe*. Studies on southern African genera such as those of Nobs (1963) on *Ceanothus* sect. *Cerastes*, a typical member of the California sclerophyll, or of Lenz (1958, 1959) on Californian species of *Iris*, should yield valuable information on this pattern of evolution for southern Africa. Since woody and perennial plants in general often form interfertile hybrids and since they predominate in southern Africa, it can almost be said with certainty that although hybrid speciation has not been demonstrated and only postulated for one genus, *Streptocarpus*, it will most likely prove significant given the diverse environments and recurring climatic changes.

POLYPLOIDY

Chromosome studies in the southern African flora are many, but widely scattered in the literature. A survey of some data suggests that the incidence of polyploidy may be generally low. As might be expected, the frequency of polyploidy is low in woody and shrubby taxa. There are no recorded polyploids in Proteaceae, *Erica*, or *Aspalathus* (Dahlgren, 1971), for example.

In herbaceous and semiherbaceous groups polyploids are recorded for many families and assume some importance. Of 88 species of Mesembryanthemoideae studied by de Vos (1947), 33 were polyploid, almost 38%, and this pattern is evident in more recent studies in Aizoaceae. In *Pelargonium* a survey of chromosome counts for southern African species indicates a similar level of polyploidy, about 30%. For *Streptocarpus* no polyploids have been found in several species counted (Hilliard & Burtt, 1971). In Compositae few polyploids have been reported: in Calenduleae (Norlindh, 1963) 1 of 17 studied; *Euryops* (Nordenstam, 1968b) only 1 of 36 species examined; *Ursinia* (Haesler, 1967) none of 8 examined; *Felicia* (Grau, 1973) 1 species and 1 subspecies of 20 studied; *Relhania* (Bremer, 1976a) none of 18 examined. In all these taxa there is a range of habit from subshrub to herbaceous perennial to annual. *Othonna*, also Compositae, provides a contrast with 5 polyploids out of 35 species examined, while diploids and polyploids occur in 4 more species (Nordenstam, 1967a). In *Nemesia* (Scrophulariaceae) the only predominantly annual genus of southern Africa well known cytologically, all 16 species examined are diploid (Fedorov, 1969).

Turning to monocots, in Iridaceae 27 species of 295 surveyed by Goldblatt (1971) are polyploid, almost 10%. The level of polyploidy is lower, about 5%, for the winter ranifall area (Cape Region and Namaqualand). In Liliaceae, a low frequency of polyploidy is also apparent in *Ornithogalum* where Pienaar (1963) recorded only 2 polyploids in 30 and in *Aloe* where Riley (1959) reported 5% polyploidy. In *Haworthia* Riley (1960) reports 16% polyploidy in the species and 39% polyploidy if infraspecific taxa are included. Only in Gramineae does polyploidy really assume importance and a survey by de Wet (1960) suggests a frequency of about 50% in one small sample.

Thus from the few examples quoted here frequency of polyploidy in southern Africa seems somewhat lower than for the world, which Stebbins (1971) estimates is in the 30–35% range. This is consistent with Stebbins's observation that frequency of polyploidy is lowest in warm temperate areas, being higher in both tropical and cold temperate regions of the world. Except for scattered families and genera, frequency of polyploidy is unknown for southern Africa, and broad comparisons are not yet possible. Sufficient data are, however, available for the subcontinent, and a thorough literature survey will surely yield much data of interest in a field as yet barely touched.

APOMIXIS

There are no large swarms of species comparable to the northern hemisphere genera *Rubus*, *Crataegus*, or *Hieracium* in southern Africa. In this region, apomixis is well known only in Gramineae (Brown, 1958; Brown & Emery, 1958). Apomixis has long been suspected in *Eragrostis* taxa, and has recently been confirmed in the *E. curvula* complex (de Winter, pers. comm.). This mode of reproduction seems likely also in the large species of *Hypoxis* (Wilsenach, 1967; Wilsenach & Papenfus, 1967), and in some bulbous Liliaceae, especially *Ledebouria* and *Drimiopsis* (Jessop, 1970, 1972). Vegetative apomixis is recorded in several Iridaceae [e.g., *Sparaxis bulbifera* (L.) Ker, *Watsonia vivipara* Mathews & L. Bol., *Homeria bulbillifera* Lewis], and is the only form of reproduction in *Watsonia bulbillifera* Mathews & L. Bol. and *Geissorhiza bolusii* Bak. (Goldblatt, 1971). There are no doubt other scattered examples in herbaceous families, but apomixis in general appears insignificant in southern Africa except for Gramineae.

SALTATIONAL SPECIATION AND ANEUPLOIDY

Saltational speciation resulting from catastrophic selection of individuals with considerable chromosomal mutation, usually including numerical change, an idea developed by Lewis (1962, 1966) (see Raven & Axelrod, 1978: 82 for summary) is usually applied to annuals, which are relatively poorly represented in southern Africa, and have not been studied biosystematically at all. Extensive aneuploid sequences occur in several perennial herbaceous groups, and chromosomal changes are implicated in speciation in these groups. Some examples are *Moraea*, *Galaxia*, and *Romulea* (Iridaceae; Goldblatt, 1976a; de Vos, 1972) and *Lachenalia* (Liliaceae; Ornduff, pers. comm.). In Compositae aneu-

ploidy has been recorded in Calenduleae (Norlindh, 1963) in the *Pentzia-"Matricaria"-Sphaeroclinium* alliance (Nordenstam, 1967b; Mitsouka & Ehrendorfer, 1972), and in *Felicia*, where reduced base numbers are correlated with the annual habit.

Introduced Plants

I have made no attempt to gather comprehensive data on introduced plants in southern Africa, and adventives have been excluded from all statistics provided. Apart from the typical spectrum of cosmopolitan and herbaceous weedy introductions, tropical and temperate, there are some unusual problems, focused mainly in the Cape Region, and these do warrant mention.

Particularly serious introductions now widely naturalized in the Cape Region are a number of woody plants mainly of Australian origin. These include *Acacia longifolia* (Jacq.) Willd., *A. saligna* (Labill.) Wendl., *A. cyclops* Cunn., and *Albizzia lophantha* (Willd.) Benth. [*A. distachya* (Vent.) MacBride] (Leguminosae); *Hakea suaveolens* R. Br. and *H. tenuifolia* (Salisb.) Domin. (Proteaceae); *Leptospermum laevigatum* F. Muell. and *Eucalyptus lehmannii* Preiss (Myrtaceae), all Australian; and the southern European *Pinus pinaster* Ait. (see summary by Hall & Boucher, 1977). All exhibit a pattern of fast regeneration after fire and grow more rapidly than the native flora. The flora in the Cape Region comprises predominantly shrubs or herbs which are often out-competed and excluded in their native habit by these aliens. Dense stands of woody introduced species are now common throughout the Cape Region, and the flora is in danger of complete replacement in many large areas and in the long term perhaps entirely. Kruger (1977) has estimated that some 60% of the fynbos, which is especially affected by this alien element has been replaced. This is an alarming figure as it means that about one quarter of the entire area of the Cape Floristic Region is now dominated to varying degrees by naturalized alien species. These especially serious weeds are mostly native in areas of infertile soils, and their success in Cape fynbos reflects their ability to thrive on such soils in the Cape Region.

Other notable naturalized introductions, also Australian, are *Acacia melanoxylon* R. Br. in forested areas of the south and east coast, again a severe competitor of the native forest flora, and *Acacia mearnsii* D. Wild., widespread in the well-watered parts of the plateau where it is sometimes conspicuous as the only tree in grasslands. The *Lantana camara* complex, introduced species of *Rubus*, *Sesbania punica* (Cav.) Benth., *Canna* species, and *Eupatorium odoratum* L. are among the particularly serious pests in disturbed areas of forest and grassland along the equable eastern coast and interior, while *Opuntia* species (Cactaceae) still cause major problems (Arnold, 1977) in dry parts of the eastern Cape. Stirton (1978) cites 63 invasive plant species, of which approximately 20 are major pests in southern Africa.

Annual and herbaceous weeds are mostly encountered in disturbed sites along roadsides, and in farmed land. Often serious in agricultural areas, they have poor capabilities of becoming permanently established in undisturbed situations and are unimportant at present in relation to the native flora.

CONSERVATION

It follows from the previous section that the floras of the Cape Region and, secondarily, also forests of the eastern part of southern Africa are being seriously affected by alien flora in addition to the usual threats from agriculture, urbanization, and pollution. The situation in the Cape Region is most severe (Esterhuysen, 1966; Taylor, 1978), especially when the other factors affecting the flora besides alien vegetation are considered. This is the part of southern Africa first settled by Europeans, and it has been under intensive cultivation for at least fifty years and much longer in some areas. Probably all sites suitable for agriculture have been or are now in use. Areas once farmed do not revert readily to natural vegetation but are often colonized by alien plants. Farmland may comprise another quarter of the area of the Cape Region, and this in effect means that the area of the Cape Region now occupied by native flora is probably less than half the total. Much of this relatively untouched area is mountainous so that the flora of lowland areas is seriously depleted, with the situation along the south and west coast especially severe.

As this is one of the richest areas floristically in the world, and as there are numerous species of very limited range, it is clear that apart from the flora as a whole, which is endangered, large numbers of species are very seriously threatened with extinction. A. V. Hall (pers. comm.) has suggested that in the Cape Region, and Karoo to the north, including all territory south of the Orange River, there are perhaps some 1,500 species seriously threatened and at least 38 presumed extinct. Taylor (1978) estimates that about 500 species in the Cape Floristic Region are threatened, and some 60 extinct. In Natal there is very little native coastal forest left as a result of the expansion of population, the use of coastal areas for recreation, and intensive agriculture, especially of sugar cane. Although this vegetation type has counterparts to the north and has relatively few endemics in southern Africa, its loss for South Africa would be disturbing. However, several important remaining forests are now conserved.

Other regions have a less vulnerable flora which is reasonably unaffected by moderate animal grazing and can reestablish itself after land is returned from agriculture. Overgrazing is, however, serious in many areas, especially in underdeveloped countries like Lesotho and Botswana (Jacot-Guillarmod, 1968, 1971; Wild, 1968) but elsewhere too, with the accompanying erosion causing irreversible changes in the flora. Changes are of course occurring in some parts of all the floristic regions of southern Africa as a result of man's use of the land, but are more subtle even though equally serious biologically in the Karoo, Kalahari, and Highveld areas. Acocks (1953) has estimated the changes in the South African flora since 1400 AD and suggests massive reduction in forest with increases in fynbos and grassland. More disturbing are his estimates of increasing desertification and spread of the Karoo flora at the expense of grassland. This trend, if continued, would by the year 2050 leave nearly half of southern Africa true desert, and semidesert flora would occupy some presently forested areas.

Southern Africa has the dubious distinction of having in the Cape Region one of the most seriously threatened floras in the world (Raven, 1977). The situation in the rest of the subcontinent is not nearly so severe, but in the Cape

Region conditions continue to deteriorate with the spread of aliens evidently uncontrolled. Much attention is being given to problems of the Cape and elsewhere (Kruger, 1977; Stirton, 1978) and conservation is actively preached though not always practiced. Unfortunately, conservation in Africa generally means conservation of fauna, sometimes even at the expense of the flora. This point of view is being countered gradually. Reserves are now being established in many places by state and local governments, while there are several botanical gardens in South Africa, almost as many as in the rest of Africa combined. Promising signs are the establishment of reserves to protect individual taxa that are seriously threatened or particularly unusual. Innumerable private reserves in the hands of farmers and other large landowners also provide small sanctuaries for native flora. Official and public consciousness of native flora is higher than it has ever been, which offers hope, but the overwhelming floral richness and diversity in southern Africa makes conservation especially difficult.

Stable and strong government is essential for the control and planning for a rapidly expanding population which at present is doubling each 25 years and will reach more than 50 million by the year 2000. Unless stability and order are maintained, pressures could well result in serious overgrazing, careless management of resources, uncontrolled utilization of remaining forests even for fuel, all of which could culminate in biological disaster for this floristically rich and unique area of the world.

Directions for the Future

The southern African flora is relatively well known, and though there are still many more species to be described and some even uncollected, undescribed taxa cannot comprise more than a tiny portion of the known total. The time is now appropriate for the cataloging of the flora, which is already well underway with the *Flora of Southern Africa*, begun in 1957 and now accelerating, with 8% of the species completed (Killick, 1976). There is also a need for more local floras, covering phytogeographic regions as well as political subdivisions, so that comparisons of local areas can be made and differences interpreted and analyzed. Good local floras are already available for Swaziland (Compton, 1976), Lesotho (Jacot-Guillarmod, 1971), Natal (Ross, 1972) and the Cape Peninsula (Adamson & Salter, 1950), and a few more checklists are available. Effective assembling of information on the flora of more than 18,500 species will undoubtedlly be tremendously helped by the current computerization of the National Herbarium in Pretoria. With this facility operative all basic data on the flora and its components would become more easily available and much of the drudgery of plant systematics should be circumvented.

Apart from the recording, cataloging, and describing of the flora by plant systematists, there is a need to begin with biosystematic, evolutionary, and population studies in southern Africa. Little research on these lines has been done as yet, although studies by Pienaar (1963), de Vos (1972), and Rourke (1972, 1976) are a notable beginning. Such work can easily be undertaken with the basic knowledge of plant species and their ranges known, if not always conveniently available in a written flora, and need not be done in conjunction with

revisionary work. In fact, as Raven (1974) has stressed, the uncoupling of evolutionary and revisionary studies would enhance progress in evolutionary and population biology. Only when a range of such studies is available will some basic questions about the flora be answered. We do not know why there should be so few annuals in southern Africa where many more would be expected to occur. Little is known from experimental evidence of the patterns of evolution and speciation in woody, herbaceous, or annual taxa. A start should be made by compiling known data on cytology and hybridization in the flora. An appreciable amount of basic cytology may have already been done but data is widely scattered.

There are also many questions on the origin of endemic and characteristic southern African plants that could be investigated in detail—the relationship and possible ancestry of *Calodendron* to the remaining, all endemic, Diosmeae; the origin and relationships of Thymelaeeae; reasons for the extraordinary richness of succulents in the flora and the evolution and speciation in Mesembryanthemoideae particularly. Equally problematic are questions on the remarkable richness of petaloid monocots in southern Africa. Explanations will remain speculative on many of these subjects until some basic and detailed population studies are made on selected groups. When a pool of such studies is available, overall trends and patterns will begin to be perceived and evaluated.

Finally, a reasonable understanding of the southern African flora will be achieved only with the help of a fossil record which is desperately incomplete at present. There are good reasons why there are fewer plant fossils in southern Africa of Tertiary age, but there are certainly many more than have been studied thus far (Martin, 1953). The assemblage from Banke in Namaqualand (Axelrod & Raven, 1978) illustrates just how valuable even a small fossil flora can be in interpreting age and relationships of the flora. A systematic search for appropriate sites for Tertiary plant fossils should yield exciting results while a reinvestigation of Banke for more material should receive priority. Only with a good understanding of the history of the flora can its present status be properly appreciated.

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Appendix 1

Families of seed plants in southern Africa, with numbers of genera, species and endemism.

Family	Number of Genera	Endemic Genera	Number of Species	Endemic Species
Acanthaceae	41	5	355	236
Achariaceae	3	3	3	3
Aizoaceae	135	113	2,021	1,987
Alismataceae	3	—	3	—
Amaranthaceae	20	3	53	20
Amaryllidaceae	17	10	199	163
Anacardiaceae	10	4	93	67
Annonaceae	8	—	13	—
Apocynaceae	16	1	39	12
Aponogetonaceae	1	—	7	4
Aquifoliaceae	1	—	1	—
Araceae	5	—	13	6
Araliaceae	3	1	11	6
Aristolochiaceae	1	—	1	—
Asclepiadaceae	60	20	605	526
Avicenniaceae	1	—	1	—
Balanitaceae	1	—	3	—
Balanophoraceae	2	1	3	2
Balsaminaceae	1	—	4	2
Basellaceae	1	—	1	—
Begoniaceae	1	—	5	3
Bignoniaceae	6	—	11	2
Bombacaceae	1	—	1	—
Boraginaceae	13	3	81	60
Bruniaceae	12	12	75	75
Burmanniaceae	1	—	1	—
Burseraceae	1	—	31	13
Buxaceae	1	—	2	2
Cabombaceae	1	—	1	—
Cactaceae	1	—	1	—
Callitrichaceae	1	—	2	—
Campanulaceae	18	11	380	350
Canellaceae	1	—	1	—
Capparaceae	8	—	49	15
Caryophyllaceae	8	—	40	30
Celastraceae	12	3	58	29
Ceratophyllaceae	1	—	1	—
Chenopodiaceae	12	2	108	92
Chrysobalanaceae	1	—	2	—
Clusiaceae	1	—	2	1
Combretaceae	5	—	35	7
Commelinaceae	6	—	28	1
Compositae	174	80	2,072	1,801
Connaraceae	2	—	2	—
Convolvulaceae	15	—	94	28

APPENDIX 1. *Continued*

Family	Number of Genera	Endemic Genera	Number of Species	Endemic Species
Cornaceae	1	—	1	—
Crassulaceae	5	2	219	194
Cruciferae	15	8	109	100
Cucurbitaceae	17	—	67	21
Cunoniaceae	2	1	2	2
Cupressaceae	1	—	3	2
Cyperaceae	30	7	421	218
Dichapetalaceae	2	—	3	—
Dioscoreaceae	1	—	17	5
Dipsacaceae	2	—	24	19
Dipterocarpaceae	1	—	1	—
Droseraceae	2	—	19	13
Ebenaceae	2	—	34	19
Elatinaceae	2	—	11	4
Ericaceae	24	19	799	797
Eriocaulaceae	2	—	11	7
Erythroxylaceae	2	—	5	3
Escalloniaceae	1	—	1	—
Euphorbiaceae	41	4	389	310
Flacourtiaceae	13	1	25	9
Flagellariaceae	1	—	1	—
Frankeniaceae	1	—	3	2
Geissolomaceae	1	1	1	1
Gentianaceae	7	1	62	47
Geraniaceae	5	—	271	261
Gesneriaceae	2	1	43	42
Goodeniaceae	1	—	2	—
Gramineae	169	21	743	330
Greyiaceae	1	1	3	3
Grubbiaceae	1	1	3	3
Gunneraceae	1	—	1	—
Haemodoraceae	4	4	12	12
Haloragidaceae	2	—	3	—
Hamamelidaceae	1	—	3	2
Hernandiaceae	1	—	1	—
Hydnoraceae	1	—	3	3
Hydrocharitaceae	4	—	11	—
Hydrophyllaceae	1	1	2	2
Hydrostachyaceae	1	—	1	—
Hypericaceae	1	—	7	4
Hypoxidaceae	6	5	83	79
Icacinaceae	3	—	6	—
Iridaceae	44	27	846	816
Illecebraceae	4	—	9	5
Juncaceae	3	1	19	6
Juncaginaceae	1	—	2	—
Labiatae	31	2	225	161
Lauraceae	4	—	11	7
Lecythidaceae	1	—	1	—
Leguminosae	115	20	1,495	1,114
Lemnaceae	6	—	9	1
Lentibulariaceae	2	—	18	1
Liliaceae	54	21	907	803
Linaceae	2	—	6	4
Loasaceae	1	—	1	1
Loganiaceae	5	—	24	5

APPENDIX 1. *Continued*

Family	Number of Genera	Endemic Genera	Number of Species	Endemic Species
Loranthaceae	12	2	54	23
Lythraceae	7	1	35	15
Malpighiaceae	3	—	13	7
Malvaceae	14	2	122	39
Melastomataceae	4	—	9	1
Meliaceae	6	1	12	1
Melianthaceae	2	1	14	12
Menispermaceae	7	1	13	4
Menyanthaceae	2	—	2	1
Monimiaceae	1	—	1	—
Montiniaceae	1	—	1	—
Moraceae	4	—	27	3
Moringaceae	1	—	1	—
Musaceae	2	—	6	4
Myricaceae	1	—	9	7
Myrothamnaceae	1	—	1	—
Myrsinaceae	4	—	7	4
Myrtaceae	4	—	8	2
Najadaceae	1	—	3	—
Neuradaceae	2	2	7	7
Nyctaginaceae	4	1	10	5
Nymphaeaceae	1	—	4	—
Ochnaceae	2	—	13	3
Olacaceae	2	—	3	—
Oleaceae	5	—	22	12
Oliniaceae	1	—	4	2
Onagraceae	3	—	11	—
Opiliaceae	1	—	1	—
Orchidaceae	54	15	461	371
Orobanchaceae	1	—	1	—
Oxalidaceae	2	—	203	199
Palmae	5	1	6	1
Papaveraceae	5	4	7	7
Passifloraceae	4	—	17	6
Pedaliaceae	8	—	29	12
Penaeaceae	7	7	21	21
Phytolaccaceae	2	—	5	—
Piperaceae	2	—	6	—
Pittosporaceae	1	—	1	—
Plantaginaceae	1	—	10	7
Plumbaginaceae	3	—	21	19
Podocarpaceae	1	—	4	2
Podostemaceae	4	—	4	—
Polygalaceae	4	1	201	176
Polygonaceae	4	—	31	14
Pontederiaceae	3	—	3	—
Portulacaceae	5	1	56	49
Potamogetonaceae	1	—	7	—
Primulaceae	3	—	7	—
Proteaceae	13	10	336	326
Ptaeroxylaceae	1	—	1	—
Rafflesiaceae	1	—	3	3
Ranunculaceae	7	—	25	14
Resedaceae	1	—	3	2
Restionaceae	12	11	316	316
Retziaceae	1	1	1	1

Appendix 1. *Continued*

Family	Number of Genera	Endemic Genera	Number of Species	Endemic Species
Rhamnaceae	9	1	156	144
Rhizophoraceae	4	—	8	2
Roridulaceae	1	1	2	2
Rosaceae	9	—	133	125
Rubiaceae	59	8	234	122
Ruppiaceae	1	—	2	—
Rutaceae	23	13	271	255
Salicaceae	1	—	5	3
Salvadoraceae	2	—	3	—
Santalaceae	6	2	144	136
Sapindaceae	13	2	23	7
Sapotaceae	7	—	14	1
Scrophulariaceae	51	16	515	447
Selaginaceae	10	7	210	204
Simaroubaceae	1	—	3	2
Solanaceae	3	—	59	44
Sphenocleaceae	1	—	1	—
Stangeriaceae	1	1	1	1
Sterculiaceae	6	—	169	143
Stilbaceae	5	5	13	13
Tamaricaceae	1	—	1	—
Tecophilaeaceae	2	1	10	9
Thymelaeaceae	8	2	179	170
Tiliaceae	4	—	49	11
Trapaceae	1	—	1	—
Turneraceae	4	—	9	1
Typhaceae	1	—	1	—
Ulmaceae	3	—	5	—
Umbelliferae	32	13	155	140
Urticaceae	11	—	27	15
Vahliaceae	1	—	2	—
Valerianaceae	2	—	2	1
Velloziaceae	2	1	9	3
Verbenaceae	9	—	55	29
Violaceae	3	—	8	3
Vitaceae	5	—	48	20
Welwitschiaceae	1	—	1	—
Xyridaceae	1	—	10	7
Zamiaceae	1	—	25	25
Zannichelliaceae	4	—	5	1
Zingiberaceae	1	—	2	—
Zosteraceae	1	—	1	—
Zygophyllaceae	7	3	46	43
TOTAL	1,859	559	18,327	14,808

Appendix 2

Genera endemic in southern Africa, with numbers of species and general distribution. A total of 559 genera are endemic in southern Africa and 190 are endemic in the Cape Floristic Region. (Abbreviations: Namaq. = Namaqualand; O.F.S. = Orange Free State; Tvl. = Transvaal; S.W. Cape includes the whole Cape Floristic Region).

Acanthaceae

Acanthopsis 8—Namibia to Karoo
Aulojusticia 1—E. Tvl.
Chaetacanthus 3—Tvl., O.F.S., Natal to S. Cape
Glossochilus 2—Tvl., Botswana, N. Cape
Mackaya 1—E. Tvl. to E. Cape

Achariaceae

Acharia 1—S. Cape (van Stadens) to Natal
Ceratosicyos 1—S. Cape (Knysna) to E. Tvl.
Guthriea 1—E. Cape to Natal

Aizoaceae

Acrodon 3—S. Cape
Acrosanthes 5—S.W. Cape
Adenogramma 10—Mainly S.W. Cape to S. Namibia, E. Cape
Aethephyllum 1—S.W. Cape
Aloinopsis 15—Mainly Karoo to N. Cape, Namaq.
Amoebophyllum 1—S.W. Cape
Amphibolia 3—W. Karoo (Tanqua), S. Namaq.
Anisocalyx 1—Namaq. (Kommagas)
Antegibbaeum 1—S. and Little Karoo
Apatesia 4—W. Cape
Aptenia 1—E. Cape coast
Argyroderma 10—S. Namaq.
Aridaria 5—S.W. Cape, Karoo to Namibia
Aspazoma 1—Namaq.
Astridia 10—N. Namaq. to S. Namibia
Bergeranthus 11—E. Cape to O.F.S.
Berrisfordia 1—Namaq. (Kamiesberg)
Bijlia 1—S. Karoo (Prince Albert)
Braunsia 3—S.W. Cape
Calamophyllum 3?—Karoo
Carpanthea 2—S.W. Cape
Carruanthus 2—S. Karoo (Willowmore)
Caryotophora 1—S. Cape (Bredasdorp)
Cephalophyllum 60—S.W. Cape, Namaq. to S. Namibia
Cerochlamys 1—Little Karoo
Chasmatophyllum 6—Karoo, O.F.S., S. Namibia
Cheiridopsis 91—W. Cape, Namaq., S. Namibia
Coelanthum 3—S.W. Cape to S. Namibia
Conicosa 10—S.W. Cape to Karoo
Conophytum 210—S.W. Cape, Namaq., Karoo, S. Namibia
Cylindrophyllum 5—S. and Little Karoo
Dactylopsis 1–2—S. Namaq. (Knersvlakte)
Dicrocaulon 6—W. Cape, Namaq.
Didymaotus 1—Ceres Karoo
Dinteranthus 4—S. Namibia, N. Cape
Diplosoma 1—W. Cape (Piketberg)
Dorotheanthus 10—S.W. Cape to Namaq.
Drosanthemum 90—Mainly S.W. Cape to S. Namibia, Karoo, and E. Cape
Eberlanzia 25—Widespread, mainly arid areas
Ebracteola 3—Namibia
Enarganthe 1—Namaq. (Richtersveld)
Erepsia 36—S.W. Cape to E. Cape
Esterhuysenia 1—S.W. Cape (Worcester)
Eurystigma 1—Ceres Karoo
Faucaria 33—S. Cape to S. Karoo, E. Cape
Fenestraria 2—Namaq. (Richtersveld) to S. Namibia
Frithia 1—Central Tvl.
Gibbaeum 15—Mainly Little Karoo to S. Karoo
Glottiphyllum 56—S.W. Cape, Karoo to E. Cape
Hereroa 34—Cape Prov., O.F.S., Namibia
Herrea 24—S.W. Cape, Namaq., W. Karoo
Herreanthus 1—Namaq. (Steinkopf)
Hymenogyne 2—W. Cape
Jacobsenia 2—S. Namaq. (Knersvlakte)
Jensenobotrya 1—S. Namibia (Lüderitz)
Juttadinteria (incl. *Dracophilus*, *Namibia*) 12—N. Namaq., S. Namibia
Kensitia 1—W. Cape (Piketberg)
Khadia 6—Tvl.
Lampranthus 72—S.W. Cape to Namaq., S. Namibia
Lapidaria 1—S. Namibia (Warmbad)
Leipoldtia 19—S.W. Cape, Namaq., S. Namibia
Lithops 40—Widespread except eastern regions
Machairophyllum 8—S.W. Cape to E. Cape
Malephora 13—S.W. Cape to Karoo, S. Namibia
Maughaniella 1—S. Namaq. (Knersvlakte)
Mestoklema 6—E. Cape, Karoo, N. Cape, S. Namibia
Meyerophytum 4—Namaq.
Micropterum 6—S.W. Cape, Namaq., Karoo
Mitrophyllum 6—S. Namaq. (Knersvlakte)
Monilaria 5—S. Namaq.
Mossia 1—S. Tvl., O.F.S.
Muiria 1—S. Cape (Riversdale)
Namaquanthus 1—Namaq.

APPENDIX 2. *Continued*

Nananthus 9—Karoo, Kalahari
Nelia 4—N. Namaq. (Richtersveld)
Neohenricia 1—Karoo
Octopoma 3—S.W. Cape to Namaq.
Odontophorus 3—Namaq. (Steinkopf)
Oophytum 2—S. Namaq. (Knersvlakte)
Ophthalmophyllum 19—Namaq., S. Namibia
Orthopterum 2—E. Cape
Ottosonderia 2—Namaq.
Pherolobus 1—W. Karoo (Calvinia)
Platythyra 1—E. Cape (Swartkops R.)
Pleispilos 33—Mainly O.F.S., Little Karoo
Plinthus 4—Widespread in arid areas
Polpoda 2—S.W. Cape
Polymita 1—Namaq. (Richtersveld)
Prenia 5—S.W. Cape to S. Namibia
Psammophora 4—N. Namaq., S. Namibia
Rabiea 7—Karoo, N. Cape, O.F.S.
Rhinephyllum 2—Karoo
Rhombophyllum 3—E. Cape, Karoo
Ruschia 326—Widespread except eastern region
Ruschianthemum 1—Namaq., S. Namibia
Ruschianthus 1—S. Namibia (Numeis)
Saphesia 1—W. Cape (Kalbaskraal)
Scletium 22—S.W. Cape, Karoo, N. Cape
Schlecteranthus 2—Namaq. (Richtersveld)
Scopelogena 2—S.W. Cape (Peninsula–Swellendam)
Semnanthe 1—S.W. Cape (Paarl–Stellenbosch)
Skiatophyllum 1—W. Cape
Smicrostigma 1—S.W. Cape
Sphalmanthus 30—S.W. Cape to S. Namibia, Karoo, O.F.S.
Stayneria 1—S.W. Cape (Worcester)
Stoeberia 2—N. Namibia (Lüderitz)
Stomatium 44—Karoo, O.F.S., N. Cape
Synaptophyllum 1—S. Namibia (Lüderitz)
Titanopsis 4—Namaq., N. Cape, S. Namibia
Vanheerdea 4—Karoo
Vanzylia 3—W. Cape to S. Namaq.
Wooley 1—Namaq. coast
Zeuktophyllum 1—S. Cape (Riversdale Karoo)

Amaranthaceae

Arthraerua 1—Namibia (Namib Desert)
Calicorema 2—Central and W. Namibia to N.W. Cape
Leucosphaera 1—Namibia, Botswana, N.W. Cape

Amaryllidaceae

Amaryllis 1—S.W. Cape
Apodolirion 4—S. Cape to E. Tvl.
Carpolyza 1—S.W. Cape
Clivia 4—E. Cape to Tvl., forests
Cybistetes 1—S.W. Cape
Gethyllis 18—S.W. Cape to Namaq.
Haemanthus 9—Widespread
Hessea 12—S.W. Cape–Namibia, Karoo
Nerine 20—Widespread, mainly E. Cape to Tvl.
Strumaria 8—Namibia, Namaq. to W. Cape

Anacardiaceae

Heeria 1—S.W. Cape
Laurophyllus 1—S.W. Cape
Loxostylus 1—S. Cape to S. Natal
Smodingium 1—Tvl. to E. Cape

Apocynaceae

Gonioma 1—S. Cape to Natal

Araliaceae

Seemanaralia 1—Tvl. to E. Cape

Asclepiadaceae

Anisotoma 2—Natal to E. Cape
Astephanus 2—C. and E. Cape to Namaq.
Cordylogyne 1—Widespread mainly in E. Highlands
Dregea 3—Widespread except in S.W. Cape
Ectadium 2—Namibia and Namaq.
Emplectanthus 2—Natal
Eustegia 5—Namaq., S.W. Cape
Fanninia 1—Natal to E. Cape
Hoodia ca. 10—Namibia, N.W. Cape, N.W. Tvl.
Huerniopsis 3—Namibia, Botswana, N. Cape
Macropetalum 1—Tvl., O.F.S.
Microloma 12—Namibia, Namaq., S.W. Cape
Oncinema 1—S.W. Cape
Orbeanthus 2—N. Tvl.–Natal Drakensberg
Parapodium 3—Tvl., O.F.S., N.E. Cape
Pectinaria 5—N.W. and Central Cape
Rhyssolobium 1—Namaq.
Sisyranthus 12—Widespread except in S.W. Cape
Stapeliopsis 2—Namibia to Namaq.
Woodia 3—Tvl. to S. Cape

Balanophoraceae

Mystropetalum 2—S.W. Cape

Boraginaceae

Echiostachys 3—S.W. Cape
Lobostemon 28—S.W. Cape, Namaq., W. Karoo
Tysonia 1—E. Cape, Natal Drakensberg

APPENDIX 2. *Continued*

Bruniaceae

Audouinia 1—S.W. Cape
Berzelia 12—S.W. Cape to E. Cape
Brunia 7—S.W. Cape
Linconia 2—S.W. Cape
Lonchostoma 5—S.W. Cape
Mniothamnea 2—S.W. Cape
Nebelia 6—S.W. Cape
Pseudobaeckia 4—S.W. Cape
Raspalia 6—S.W. Cape, Natal
Staavia 10—S.W. Cape
Thamnea 7—S.W. Cape
Tittmannia 4—S.W. Cape

Campanulaceae

Grammatotheca 1—S.W. Cape (? introd. to Australia)
Merciera 4—S.W. Cape
Microcodon 4—S.W. Cape
Namacodon 1—Namib Desert
Prismatocarpus 30—Mainly S.W. Cape to Namaq., E. Cape
Rhigiophyllum 1—S.W. Cape
Roella 24—Mainly S.W. Cape to E. Cape
Siphocodon 2—S.W. Cape
Theilera 1—S.W. Cape
Treichelia 1—S.W. Cape
Unigenes 1—S.W. Cape

Celastraceae

Hartogia 1—Tvl. to S.W. Cape
Maurocenia 1—S.W. Cape
Pseudosalacia 1—S. Natal

Chenopodiaceae

Exomis 1—Namaq., Karoo, Namibia
Manochlamys 1—Namibia, Namaq., S.W. Cape

Compositae

Adenanthemum 1—E. Tvl. highveld
Adenoglossa 1—Namaq.
Alatoseta 1—S. Karoo (Laingsburg)
Alciope 2—S.W. Cape
Amellus 12—S.W. Cape to Namibia, Karoo
Amphiglossa 4—S.W. Cape to Namibia
Anaxeton 9—S.W. Cape
Anisochaeta 1—Transkei to Natal
Anisothrix 1—S.W. Cape (Montagu)
Antiphiona 2—Namibia
Antithrixia 1—Namaq.
Arrowsmithia 1—E. Cape (King Williams Town)
Asaemia 2—Margin of S.W. Cape to Namibia
Brachymeris 6—Tvl., Swaziland
Bryomorphe 1—S.W. Cape
Cadiscus 1—W. Cape (Malmesbury)
Callilepis 5—Tvl. to E. Cape
Castalis 3—S.W. Cape, Tvl.
Comptonanthus 3—S.W. Cape (Witteberg) to Karoo and Namibia
Corymbium 10—Mainly S.W. Cape to E. Cape
Cullumia 15—S.W. Cape to Karoo
Cuspidia 1—S. Cape to Karoo, E. Cape
Cymbopappus 3—S.W. Cape, Natal, E. Tvl.
Didelta 2—W. Cape, Namaq., Namibia
Disparago 7—Mainly S.W. Cape to E. Cape
Dymondia 1—S. Cape (Bredasdorp)
Elytropappus 8—Mainly S.W. Cape to Namaq., S. Karoo, E. Cape
Engleria 2—Namibia
Eremothamnus 1—S. Namib Desert
Eriosphaera 1—Karoo and O.F.S.
Eroeda 6—Mainly S.W. Cape to E. Cape
Eumorphia 5—Karoo Mts. to Drakensberg
Garuleum 8—Widespread except S.W. Cape
Gibbaria 2—S.W. Cape
Gorteria 3—Namibia to S.W. Cape
Gymnodiscus 2—Namaq. to S.W. Cape
Gymnopentzia 1—Drakensberg
Gymnostephium 7—S.W. Cape
Heterolepis 3—S.W. Cape
Heteromma 3—Drakensberg
Heterorhachis 1—W. Cape
Hippia 6—Mainly S.W. Cape to E. Cape
Hoplophyllum 2—Namaq. to Karoo
Inezia 1—E. Tvl., Swaziland
Lachnospermum 2—S.W. Cape to Namaq.
Lamprocephalus 1—S.W. Cape
Leontonyx 6—Widespread
Lepidostephium 1—E. Cape
Leucoptera 3—S.W. Cape to Namaq.
Lidbeckia 2—W. Cape
Mairia 21—S.W. Cape
Marasmodes 5—S.W. Cape
Metalasia 33—Mainly S.W. Cape, E. Cape to Natal
Minurothamnus 1—S.W. Cape (Caledon)
Oldenburgia 4—S.W. Cape to E. Cape
Oligothrix 1—W. Cape
Ondetia 1—Namibia (Damaraland)
Osmitopsis 9—S.W. Cape
Oxylaena 1—S. Cape
Pentatrichia 3—Namibia, Karoo, N. Tvl.
Perdicium 2—W. Cape
Petalacte 2—S.W. Cape
Peyrousea 1—S.W. Cape
Phaenocoma 1—S.W. Cape
Phaeocephalus 1—S.W. Cape (Swartberg and Witteberg)
Phaneroglossa 1—S.W. Cape
Philyrophyllum 1—Tvl.

APPENDIX 2. *Continued*

Phymaspermum 6—Karoo to Namaq.
Platycarpha 3—Namibia to N. Cape, Karoo, Natal
Poecilolepis 2—Cape Peninsula to E. Cape
Polyarrhena 4—S.W. Cape
Printzia 7—S.W. Cape to Drakensberg
Psednotrichia 1—S.W. Cape to Namaq.
Pterothrix 4—Namibia to Karoo
Relhania 29—S.W. Cape, Karoo, Namaq., Natal
Rhynea 1—E. Cape to Tvl.
Rosenia 4—S.W. Cape, Karoo, Namaq.
Stilpnogyne 1—S.W. Cape
Stilpnophytum 4—S.W. Cape
Thaminophyllum 3—S.W. Cape

Crassulaceae

Andromischus 30—Widespread
Tylecodon 26—Widespread

Cruciferae

Aplanodes 2—Natal, E. Cape, Lesotho
Brachycarpaea 1—S.W. Cape to Namaq.
Chamira 1—S.W. Cape
Cycloptychis 2—W. Cape
Heliophila 71—Mainly S.W. Cape to Tvl.
Schlecteria 1—W. Cape (Cedarberg)
Silicularia 1—W. Cape (Ceres)
Thlaspeocarpa 2—Namaq., W. Karoo, W. Cape

Cunoniaceae

Platylophus 1—S. Cape

Cyperaceae

Chrysithrix 2—S.W. Cape
Epischoenus 8—S.W. Cape to E. Cape
Hellmuthia 1—S. Cape
Macrochaetium 2—S.W. Cape to Natal
Neesenbeckia 1—S.W. Cape
Trianopteles 3—S.W. Cape
Volkiella 1—N. Namibia

Ericaceae

Acrostemon 12—S.W. Cape
Aniserica 2—S.W. Cape
Anomalanthus 10—S.W. Cape
Coccosperma 4—S.W. Cape
Coilostigma 4—S. Cape
Eremia 7—S.W. Cape
Eremiella 1—S. Cape (Outeniqua Mts.)
Grisebachia 9—S.W. Cape
Lepterica 1—S.W. Cape
Nagelocarpus 2—S.W. Cape
Platycalyx 1—S. Cape (Riversdale)
Salaxis 8—S.W. Cape
Scyphogyne 18—S.W. Cape
Simocheilus 21—S.W. Cape
Stokoeanthus 1—S.W. Cape
Sympieza 8—S.W. Cape
Syndesmanthus 19—S.W. Cape
Thamnus 1—S. Cape
Thoracosperma 12—S.W. Cape

Euphorbiaceae

Ctenomeria 1—S. Cape to E. Mts.
Hyenanche 1—W. Cape (Clanwilliam to Nieuwoudtville)
Lachnostylis 2—S.W. Cape
Seidelia 3—E. Cape, Karoo, O.F.S.

Flacourtiaceae

Pseudoscolopia 1—S.W. Cape to Natal

Geissolomaceae

Geissoloma 1—S. Cape (Langeberg)

Gentianaceae

Orpheum 1—S.W. Cape

Gesneriaceae

Charadrophila 1—W. Cape (Stellenbosch distr.)

Gramineae

Catalepis 1—Drakensberg to E. Tvl.
Chaetobromus 4—S.W. Cape to Namaq.
Dregeochloa 2—S. Namibia to Karoo
Harpochloa 1—E. Mts. and highveld
Kaokochloa 1—Namibia
Karoochloa 4—S.W. Cape, E. Cape, Karoo
Lasiochloa 5—Mainly S.W. Cape to Karoo
Leucophrys 4—Central Namibia
Lophacme 1—Tvl. highveld
Mosdenia 1—N. Tvl.
Pentameris 6—S.W. Cape
Plagiochloa 5—S.W. Cape
Poagrostis 1—S.W. Cape
Polevansia 1—Drakensberg
Prionanthium 3—S.W. Cape
Prosphytochloa 1—E. Cape to Tvl.
Pseudopentameris 2—S.W. Cape
Psilochloa 1—N. Namibia
Tarigidia 1—Namibia, N. Cape, O.F.S.
Tetrachne 1—Drakensberg
Urochlaena 1—S.W. Cape, Karoo

Greyiaceae

Greyia 3—Tvl. to E. Cape

APPENDIX 2. *Continued*

Grubbiaceae

Grubbia 3—S.W. Cape

Haemodoraceae

Barberetta 1—E. Cape, Natal
Dilatris 5—S.W. Cape
Lanaria 1—S.W. Cape, E. Cape
Wachendorfia 5—S.W. Cape

Hydrophyllaceae

Codon 2—Namaq. to Namibia

Hypoxidaceae

Empodium 9—Tvl. to S.W. Cape
Pauridia 2—S.W. Cape
Rhodohypoxis 6—Drakensberg
Saniella 1—Drakensberg
Spiloxene 30—S.W. Cape to Namaq.

Iridaceae

Gen. nov. 1—W. Karoo
Anapalina 7—S.W. Cape to E. Cape
Anomalesia 3—S.W. Cape to Namibia
Antholyza 2—S.W. Cape to Namaq.
Barnardiella 1—Namaq.
Bobartia 15—Mainly S.W. Cape to S. Natal
Chasmanthe 4—Mainly S.W. Cape to Namaq.
Duthieastrum 1—W. Tvl. to N.W. Cape
Engysiphon 10—Mainly S.W. Cape to Namaq.
Freesia 19—S.W. Cape, E. Cape, Karoo to W. Tvl.
Galaxia 12—S.W. Cape to Namaq.
Geissorhiza 60—Mainly S.W. Cape to Namaq.
Hexaglottis 4—S.W. Cape to Namaq.
Homeria 30—Widespread, mainly S.W. Cape and Namaq.
Homoglossum 10—Mainly S.W. Cape to E. Cape
Ixia 45—S.W. Cape to Namaq. and E. Cape
Klattia 2—S.W. Cape
Micranthus 3—S.W. Cape
Nivenia 8—S.W. Cape
Pillansia 1—S.W. Cape (Caledon distr.)
Sparaxis 6—S.W. Cape
Synnotia 5—Mainly S.W. Cape to S. Namaq.
Syringodea 8—Arid parts of S.W. Cape, Karoo, S. Tvl.
Thereianthus 7—S.W. Cape
Tritoniopsis 14—S.W. Cape
Watsonia 70—S.W. Cape to Namaq., E. areas
Witsenia 1—S.W. Cape

Juncaceae

Prionum 1—S.W. Cape to Natal

Labiatae

Syncolostemon 9—Transkei to Tvl.
Thorncroftia 3—E. and N. Tvl.

Leguminosae

Amphithalea 16—Mainly S.W. Cape to E. Cape
Aspalathus 255—Mainly S.W. Cape to Namaq., E. Cape, Natal
Bolusafra 1—S.W. Cape
Buchenroedera 20—S.W. Cape, S. Tvl., Natal, E. Cape
Chrysoscias 6—S.W. Cape to Tvl.
Coelidium 15—S.W. Cape
Cyclopia 20—S.W. Cape
Dipogon 1—S.W. Cape to E. Cape
Hypocalyptus 3—S.W. Cape
Lebeckia 39—S.W. Cape to Namaq., Namibia, Natal
Liparia 2—S.W. Cape
Melolobium 20—Widespread, mainly arid areas
Podalyria 22—Mainly S.W. Cape to E. Cape
Priestleya 20—S.W. Cape
Rafnia 22—S.W. Cape to S. Natal
Sutherlandia 5—Widespread
Umtiza 1—E. Cape coast
Virgilia 2—S.W. Cape mainly in south
Wiborgia 10—S.W. Cape to Namaq. and W. Karoo
Xerocladia 1—Namaq., Namibia

Liliaceae

Agapanthus 10—S.W. Cape, E. Cape to Tvl.
Amphisiphon 1—S.W. Cape (Nieuwoudtville)
Androsiphon 1—S.W. Cape (Nieuwoudtville)
Baeometra 1—S.W. Cape
Daubenya 1—W. Karoo (Sutherland)
Dipidax 3—S.W. Cape
Galtonia 3—Transkei to Drakensberg
Gasteria prob. 15—S.W. Cape to Namaq., E. Cape
Hexacyrtis 1—Namib Desert
Lachenalia 80—Mainly S.W. Cape to Namaq., Karoo
Litanthus 1—Widespread
Massonia 8—S.W. Cape to Namaq., Karoo
Neodregea 1—S.W. Cape to E. Cape
Neopatersonia 3—S.W. Cape to Namaq.
Poellnitzia 1—S.W. Cape (Worcester to Robertson)
Polyxena 2—S.W. Cape to E. Cape, Namaq., Karoo

APPENDIX 2. *Continued*

Rhadamanthus 9—S.W. Cape, Namaq., Namibia
Sandersonia 1—E. Cape to E. Tvl.
Schizobasis 1—Widespread except S.W. Cape
Veltheimia 2—S.W. Cape to Namaq., E. Cape
Whiteheadia 1—Namaq., Namibia

Loranthaceae

Moquiniella 1—S.W. Cape, Karoo, E. Cape
Septulina 2—S.W. Cape, Namaq., S. Namibia

Lythraceae

Rhynchocalyx 1—Natal S. coast

Malvaceae

Anisodontea 19—Mainly S.W. Cape to Namaq., O.F.S., Natal
Radyera 1—Namibia, Namaq., Karoo, O.F.S.

Meliaceae

Nymania 1—S. Cape (Little Karoo) to Namibia

Melianthaceae

Melianthus 8—Widespread, mainly arid regions

Menispermaceae

Antizoma 3—Widespread

Neuradaceae

Grielum 6—Widespread in arid areas
Neuradopsis 1–2—N. Cape, Namibia, Botswana

Nyctaginaceae

Phaeoptilum 1—Namibia to N. Cape

Orchidaceae

Acrolophia 7—Mainly S.W. Cape, Natal
Amphigena 2—S.W. Cape
Anochilus 3—S.W. Cape to E. Cape
Bartholina 2—S.W. Cape to E. Cape
Ceratandra 3—Mainly S.W. Cape to E. Cape
Corycium 17—Mainly S.W. Cape to E. Tvl.
Evota 3—S.W. Cape
Forficaria 2—S.W. Cape
Huttonaea 4—E. Cape to Tvl.
Monadenia 21—Mainly S.W. Cape to E. Cape, E. Tvl.
Orthopenthea 12—S.W. Cape
Pachites 2—S.W. Cape
Penthea 2—S.W. Cape
Satyridium 1—S.W. Cape
Schizodium 5—S.W. Cape

Palmae

Jubaeopsis 1—Pondoland

Papaveraceae

Cysticapnos 1—S.W. Cape to Namaq.
Discocapnos 1—S.W. Cape
Phacocapnos 3—S.W. Cape to Natal
Trigonocapnos 1—W. Cape to W. Karoo

Penaeaceae

Brachysiphon 4—S.W. Cape (Peninsula to Swellendam)
Endonema 2—S.W. Cape (Riviersonderend Mts.)
Glischrocolla 1—S.W. Cape (Hottentots Holland)
Penaea 3—S.W. Cape
Saltera 1—S.W. Cape (Peninsula to Bredasdorp)
Sonderothamnus 2—S. Cape (Caledon to Bredasdorp)
Stylapterus 8—S.W. Cape

Polygalaceae

Nylandtia 1—S.W. Cape to Namaq., E. Cape

Portulaceae

Portulacaria 2—S.W. Cape, Namaq., Karoo, E. Cape

Proteaceae

Aulax 3—S.W. Cape
Brabeium 1—S.W. Cape
Diastella 7—S.W. Cape
Leucadendron 80—Mainly S.W. Cape to Natal
Mimetes 12—S.W. Cape
Orothamnus 1—S.W. Cape (Caledon)
Paranomus 18—S.W. Cape
Serruria 50—S.W. Cape
Sorocephalus 11—S.W. Cape
Spatalla 20—S.W. Cape

Restionaceae

Anthochortus 1—S.W. Cape
Calopsis (non *Leptocarpus*) 27—Mainly S.W. Cape to Natal, Namaq.
Cannomois 9—Mainly S.W. Cape, E. Cape
Chondropetalum 23—Mainly S.W. Cape to E. Cape
Elegia 36—Mainly S.W. Cape to E. Cape

APPENDIX 2. *Continued*

Hypodiscus 14—S.W. Cape
Mastersiella (non *Hypolaena*) 31—S.W. Cape
Phyllocomos 1—S.W Cape
Staberoha 9—S.W. Cape
Thamnochortus 31—Mainly S.W. Cape to Namaq., E. Cape
Willdenowia 7—S.W. Cape to Namaq.

Retziaceae

Retzia 1—S.W. Cape (Stellenbosch to Bredasdorp)

Rhamnaceae

Noltia 1—S.W. Cape to Natal

Roridulaceae

Roridula 2—S.W. Cape

Rubiaceae

Burchellia 1—S. Cape to E. Tvl.
Carpacoce 4—S.W. Cape to E. Cape
Crocyllis 1—Namibia, Namaq.
Dinocanthium 1—Tvl. to N. Natal
Eriosemopsis 1—Natal, Transkei
Galopina 3—S.W. Cape to Natal, E. Tvl.
Nenax 4—S.W. Cape to Namaq., Karoo, Namibia
Plectroniella 2—Tvl. to Natal

Rutaceae

Acmadenia 22—Mainly S.W. Cape to E. Cape
Adenandra 18—S.W. Cape
Agathosma 137—Mainly S.W. Cape to Natal
Coleonema 7—S.W. Cape
Diosma 27—Mainly S.W. Cape, Namaq.
Empleuridum 1—S.W. Cape (Caledon)
Empleurum 2—S. Cape
Euchaetes 27—S.W. Cape
Macrostylis 11—S.W. Cape
Phyllosma 2—W. Cape (Cold Bokkeveld)
Gen. nov. 1 1—W. Cape
Gen. nov. 2 4—W. Cape
Gen. nov. 3 1—S.W. Cape

Santalaceae

Rhoiacarpos 1—S.W. Cape to Transkei
Thesidium 8—Mainly S.W. Cape to E. Cape

Sapindaceae

Hippobromus 1—S. Cape to Natal, Tvl.
Smelophyllum 1—S. Cape forests

Scrophulariaceae

Antherothamnus 1—N. Cape to Namibia, Tvl.
Bowkeria 3—E. Cape to S.E. Tvl.
Colpias 1—Namaq. to W. Karoo
Diascia 53—Widespread
Dermatobotrys 1—Natal to Transkei
Dintera 1—N. Namibia (Otjiwarongo)
Glumicalyx 6—Drakensberg
Hemimeris 4—S.W. Cape to Namaq., Karoo
Hyobanche 7—S.W. Cape to Namaq., Namibia, Natal
Ixianthes 1—W. Cape
Manuleopsis 1—Namibia
Oftia 3—S.W. Cape to Namaq.
Phygelius 2—E. Cape to Tvl.
Polycarena 42—Widespread, mainly S.W. Cape
Strobilopsis 1—Drakensberg
Teedia 2—S.W. Cape, Namaq., E. Cape

Selaginaceae

Agathelpis 3—S.W. Cape
Cromidon 1—S. Karoo (foot of Witteberg)
Dischisma 11—Mainly S.W. Cape to Namaq., S. Namibia
Globulariopsis 1—S.W. Cape (Witteberg)
Gosella 1—S.W. Cape
Microdon 5—S.W. Cape
Tetraselago 4—Natal to E. Tvl.

Stangeriaceae

Stangeria 1—S.E. coast

Stilbaceae

Campylostachys 1—S.W. Cape (Peninsula to Hermanus)
Eurylobium 1—S.W. Cape (Riversonderend Mts.)
Euthystachys 1—S.W. Cape (Franch Hoek)
Stilbe 8—S.W. Cape
Xeroplana 2—S. Cape (Caledon to Riversdale)

Tecophilaeaceae

Cyanella 8—Mainly S.W. Cape to W. Karoo, Namaq., Namibia

Thymelaeaceae

Cryptadenia 5—S.W. Cape
Lachnaea 25—Mainly S.W. Cape to Namaq., Natal

Umbelliferae

Arctopus 3—S.W. Cape to Namaq.
Annesorrhiza 8—Widespread
Chamarea 1—Widespread in South Africa
Choritaenia 1—Karoo, Kalahari

Appendix 2. *Continued*

Glia 1—S.W. Cape
Hermas 6—S.W. Cape
Heteroptiles 1—S.W. Cape to Natal
Marlothiella 1—Namib Desert
Phlyctidocarpa 1—N. Namibia
Polemannia 3—S.W. Cape to Natal
Rhyticarpus 3—S.W. Cape to E. Cape
Sonderina 5—S.W. Cape to Namibia, Natal
Thunbergiella 1—S.W. Cape

Velloziaceae
T'albotia 1—E. Tvl., Natal

Zygophyllaceae
Augea 1—Namaq., Karoo
Neoleuderitzia 1—S. Namibia
Sisyndite 1—Namaq. to S. Namibia

Appendix 3

Checklist of genera of seed plants shared between tropical Africa (-S. Arabia) and southern Africa. Asterisk indicates genera with very limited ranges outside southern Africa.

Acanthaceae
Angkalanthus
Crabbea
Duosperma
Macrorungia
Megalochlamys
Ruelliopsis
Ruspolia
Ruttya
Sclerochiton
Aizoaceae
**Aizoanthemum*
Delosperma (also Reunion)
Galenia
Hypertelis
**Pharnaceum*
**Psammotropha*
**Psilocaulon*
Tribulocarpus
Alismataceae
Burnatia
Amaranthaceae
Achyropsis
Centema
Centemopsis
Cyphocarpa
**Hermbstaedtia*
Marcelliopsis
Nelsia
Pandiaka
Sericocoma
Amarylllidaceae
Ammocharis
Boophone
Brunsvigia
Cyrtanthus
Scadoxus
Anacardiaceae
**Harpephyllum*
Ozoroa
Annonaceae
Monodora
Apocynaceae
Acokanthera
Adenium
Diplochynchus
Ephippiocarpa
Araceae
Gonatopus
Stylochiton
**Zamioculcas*
Zantedeschia
Araliaceae
Cussonia
Asclepiadaceae
Curroria
Duvalia
Echidnopsis
Fockea
Huernia
Kanahia
Mondia
Orbea
**Orbiopsis*
Pachycarpus
**Pachycymbium*
Pentarrhinum
Periglossum
Piaranthus
Raphionacne
Schizoglossum
Sphaerocodon
Stapelia
Stigmatorhynchus
Stomatostemma
Tacazzea
Tavaresia
Tenaris
Xysmalobium
Balanophoraceae
Sarcophyte
Bignoniaceae
**Catophractes*
Kigelia
**Podranea*
Tecomaria
Boraginaceae
Wellstedia
Canellaceae
Warburgia
Campanulaceae
Cyphia
Monopsis
Capparaceae
**Bachmannia*
Cladostemon
Caryophyllaceae
Krauseola
Celastraceae
Allocassine
Catha
**Putterlickia*
Pterocelastrus
Chenopodiaceae
Lophiocarpus
Combretaceae
Pteleopsis
Compositae
Arctotheca
Arctotis
Artemesiopsis
Berkheya
Bothriocline
Calostephane
Chrysanthemoides
**Chrysocoma*
Denekia
**Dimorphotheca*
Eriocephalus

APPENDIX 3. *Continued*

Erlangea
Euryops
Felicia
Gazania
Geigeria
Gerbera
Gongrothamnus
Haplocarpha
Hirpicium
Kleinia
**Leontonyx*
Lopholaena
Macowania
Nicolasia
**Othonna*
**Pechuel-loeschea*
Pentzia
Pleiotaxis
Pteronia
Schistostephium
**Sphaeroclinum*
Stomatanthes
Tarchonanthus
Ursinia
Convolvulaceae
Astripomoea
Falkia
Cornaceae
**Curtisia*
Crassulaceae
Cotyledon
Cucurbitaceae
Acanthosicyos
Gerrardanthus
Trochomeria
Cupressaceae
Widdringtonia
Cyperaceae
Ficinia
Dipterocarpaceae
Monotes
Ebenaceae
Euclea
Ericaceae
Blaeria
Ericinella
Erythroxylaceae
Nectaropetalum
Escalloniaceae
Choristylis
Euphorbiaceae
**Adenocline*
Cavacoa
Clutia
Erythrococca
Heywoodia
Leidesia
Monadenium
Pseudolachnostylis
Pterococcus
Ricinodendron
Spirostachys
Synadenium
Flacourtiaceae
Gerrardina
Kiggelaria
Oncoba
Rawsonia
Trimeria
Xylotheca
Geraniaceae
**Sarcocaulon*
Gramineae
Beckeropsis
Bewsia
Cleistachne
Cymbosetaria
Cypholepis
Danthoniopsis
Diheteropogon
Dinebra
Ehrharta
Elymandra
Entolasia
Entoplocamia
Fingerhuthia
**Heterocarpha*
Lintonia
Megaloprotachne
Melinis
Miscanthidium
Monelytrum
Monocymbium
Odontelytrum
Odyssea
Oryzidium
Oxytenanthera
Pogonarthria
Rendlia
Sartidia
Schmidtia
Stiburus
Stereochlaena
Streblochaete
Styppeiochloa
Urelytrum
Urochloa
Hamamelidaceae
Trichocladus
Illecebraceae
Pollichia
Iridaceae
Anomatheca
Babiana
Crocosmia
Dierama
Ferraria
Hesperantha
Lapeirousia
Moraea
Oenostachys
Radinosiphon
Schizostylis
Tritonia
Labiatae
Acrotome
Aeolanthus
Becium
Englerastrum
Hemizygia
Holostylon
Hoslundia
Iboza
Tinnea
Leguminosae
**Adenolobus*
Amblygonocarpus
Baikiaea
Bolusia
Bolusanthus
Brachystegia
Burkea
Colophospermum
Craibia
Dichilus
Elephantorrhiza
Julbernardia
Lablab
Lessertia
Neorautanenia
Otoptera
Ptycholobium
Requienia
**Schotia*
Tylosema
Xeroderris
Lemnaceae
Pseudowolffia
Liliaceae
Albuca
**Behnia*
**Bowiea*
Bulbine
**Camptorrhiza*
Drimiopsis
Eriospermum
**Eucomis*
**Haworthia*
Littonia
Ornithoglossum
Pseudogaltonia
Schizobasis
Trachyandra
Tulbaghia

APPENDIX 3. *Continued*

Loganiaceae
**Gomphostigma*
Loranthaceae
**Actinanthella*
Erianthemum
Odontella
**Pedistylis*
Plicosepalus
Tapinanthus
**Tieghemia*
**Vanwykia*
Lythraceae
**Galpinia*
Hionanthera
Malpighiaceae
Triaspis
Melastomataceae
Dissotis
Melastomastrum
Meliaceae
**Entandrophragma*
Pseudobersama
Melianthaceae
Bersama
Menispermaceae
Epinetrum
Montiniaceae
**Montinia*
Moraceae
Cardiogyne
Musaceae
Strelitzia
Monimiaceae
Xymalos
Myrtaceae
Heteropyxis
Oliniaceae
Olinia
Orchidaceae
Ansellia
Bolusiella
Bonatea
Centrostigma
Cystorchis
Diaphananthe
Herschelia
Holothrix
Mystacidium
Neobolusia
Pterygodium
Rangaeris
Schizochilus
Stenoglottis
Passifloraceae
Basananthe
Schlechterina
Pediaceae
Ceratotheca
Dicerocaryum
Holubia
Harpagophytum
Pleurodiscus
Rogeria
Sesamothamnus
Plumbaginaceae
Dyerophytum
Podostemaceae
Leiothylax
Sphaerothylax
Polygalaceae
Muraltia
Portulacaceae
Ceraria
Proteaceae
**Leucospermum*
Protea
Ptaeroxylaceae
Ptaeroxylon
Ranunculaceae
Knowltonia
Rosaceae
Cliffortia
**Leucosidea*
Rubiaceae
Amphiasma
Ancylanthus
Conostomium
Crossopteryx
Fadogia
Ferretia
Heinsia
Kraussia
Lagynias
Leptactinia
Mitrocarpum
Mitriostigma
Neorosea
Oxyanthus
Pachystigma
Pentanisia
Plectroniella
Pygmaeothamnus
Rothmannia
Tapiphyllum
Vangueriopsis
Zygoon
Rutaceae
Calodendrum
Citropsis
Oricia
Toddaliopsis
Santalaceae
Colpoon
Osyridiocarpus
Sapindaceae
Blighia
Pancovia
Pappea
Sapotaceae
Bequaertiodendron
Inhambanella
Vitellariopsis
Scrophulariaceae
Aptosimum
**Anastrabe*
Buttonia
Cycnium
Freylinia
Gerardiina
Hiernia
Ilysanthes
Manulea
Nemesia
Peliostomum
Stemodiopsis
Sutera
Zaluzianskya
Selaginaceae
Selago
Simaroubaceae
Kirkia
Sterculiaceae
Cola
Tecophilacaceae
Walleria
Thymelaeaceae
**Passerina*
Struthiola
Turneraceae
Streptopetalum
Tricliceras
Umbelliferae
Alepidia
Lefeburea
Steganotaenia
Welwitschiaceae
**Welwitschia*
Zamiaceae
Encephalartos

SOME ASPECTS OF THE PHYTOGEOGRAPHY OF TROPICAL AFRICA[1]

J. P. M. Brenan[2]

Abstract

The area covered follows political boundaries and amounts to just over 20,000,000 km². The flora is estimated at about 30,000 species and 2,497 genera. The phytogeographical affinities of the families and genera are analyzed and discussed, as is the comparative poverty of the flora. The main phytogeographical regions and domains are briefly described. The phytogeography and endemism of the rain forest flora are analyzed and discussed and some comparison is made with the savanna. The distribution of *Indigofera* species is analyzed and conclusions drawn. An attempt is made to discuss and assess the endemism at specific and generic levels shown by each country in the area, with representative examples and notes on areas of special interest. Especially high concentrations are shown in Cameroon and Gabon, Zaïre, Ethiopia, Somalia, Tanzania, and Angola. A preliminary map is given to show relative densities of endemism.

Africa has many features in its plant life and elsewhere that combine to make the continent outstanding if not unique among other tropical landmasses. However, these features are not at first sight obvious: the general shape of Africa is undistinguished if not rather dull; so is its topography—there are no great mountain masses to compare with the Andes or Himalayas, and its highest peak, Kilimanjaro, is an isolated volcanic cone that would be no more than "a considerable protuberance" in those great ranges; the flora is not especially rich, and indeed often more noteworthy for its poverty. Yet its fascination is perennial, and not without cause did Richards (1973) entitle a paper "Africa, the 'Odd Man Out'."

Poverty and change are perhaps too often the keynotes. Almost everywhere evidence of change is only too obvious: relics of forest disappearing in a sea of grass; senile trees without offspring on the edge of semidesert; lean and hungry livestock pursuing the retreating remains of grazing. Sometimes the pace is slower; only occasionally is ecological change for the better. The remarkable pictorial record of Shantz & Turner (1958) is often revealing. The flora itself and its distribution constantly show evidence of gigantic and destructive climatic changes in the past—evidence in the form of floristic poverty, spectacular

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[1] Some acknowledgements are made in the appropriate place in the paper (p. 459). I would, however, also like to express my thanks especially to Mr. P. S. Green, Deputy Director and Keeper of the Herbarium, Royal Botanic Gardens, Kew, Dr. R. Polhill and Dr. G. Wickens for much help unstintedly given and for the opportunity of discussing problems. I am also grateful to Mrs. J. Carter and Mr. T. A. Harwood for help with photography. To my wife, Jean, and my daughter, Miss Mary Brenan, my especial thanks for their help and patience during the work of preparation. I am also grateful to Dr. F. Demaret and Dr. P. Bamps for kind permission to reproduce the map of Zaïre showing vegetation boundaries originally published in the *Flore du Congo Belge et du Ruanda-Urundi*. It will of course be obvious that certain place names on this map are now superseded. Last, but far from least, my gratitude and thanks to Dr. Peter Raven for providing the opportunity and stimulus for this paper.

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Ann. Missouri Bot. Gard. 65: 437–478. 1978.

0026-6493/78/0437–0478/$04.25/0

disjunctions in distribution, islands of floristic similarity now distantly isolated, close affinities among species now widely separated geographically, etc. The details about how these changes occurred are still mostly unknown, but they seem the only possible explanation of many of today's problems.

Especially during the last fifty years, investigation of the flora and vegetation of Africa, both in the field and the herbarium, has been intense. Numerous countries have participated, and that this research has been carried out in a spirit of cooperation rather than rivalry during the past quarter-century has in large measure been due to the vision of those who founded the Association pour l'Étude Taxonomique de la Flore d'Afrique Tropicale (A.E.T.F.A.T.), still flourishing and with a scientific message as relevant today as when it started.

Although very much still remains to be done and many areas are still poorly explored botanically or even quite unknown, nevertheless Africa must now rank among the comparatively better known tropical land-areas in terms of flora and vegetation.

Few attempts, however, have been made to assess or analyze the flora as a whole. The available knowledge of the taxonomy and distribution of the African flora is now probably sufficient, although much of it is still unpublished, to allow assessments to be made of its size and richness; of its geographical affinities; of its endemism; and even of the distribution of endemism in relation to phytogeographical regions and countries. The speed of change in the vegetation of Africa is accelerating rather than diminishing, and the urgency for action over conservation has become even more acute since the publication of the proceedings of the A.E.T.F.A.T. Symposium held in Uppsala in 1966 on the Conservation of Vegetation in Africa South of the Sahara (Hedberg & Hedberg, 1968). In the present paper, with its manifest omissions and imperfections, an attempt is made to discuss and analyze some of these features of the African flora, in the hope that in the future a more complete general assessment may become feasible.

Boundaries of Area

Although tropical Africa appears in the title of this paper, the boundaries of the area under discussion here do not strictly follow the lines of the tropics. So much of the available data are based on areas demarcated by political rather than biological or climatic boundaries, that it seemed necessary to accept this situation. Accordingly, discussion took place with my cocontributors to this Symposium, Dr. P. Goldblatt of the Missouri Botanical Garden and Professor P. Quézel of the Université de Droit, d'Économie et des Sciences d'Aix-Marseille, to determine the working boundaries to the south and north respectively.

To the south, all countries to the south of Angola, Zambia, Rhodesia, and Mozambique are covered by Dr. Goldblatt's paper. To the north, Professor Quézel deals with all territories to the north of Senegal, Mali, Niger, Chad, and Sudan. The only predominantly tropical country thus excluded is Mauritania in the north. The total area covered is just under 20,000,000 km^2 (7,700,000 mi^2).

Size and Poverty of the Tropical African Flora

The relative poverty of the tropical African flora has repeatedly been noted as long ago as, for example, Mildbraed (1922: 103). A recent more detailed analysis is given by Richards (1973) who considers tropical Africa as phytogeographically an "odd man out" in comparison with the other main tropical areas of the world. He considers three differences as most significant:

(1) The relative poverty of the African flora compared with those of other comparable tropical areas,

(2) The wide areas of distribution of numerous African species, and

(3) The poverty (or absence) in tropical Africa of certain plant groups.

Let us deal more fully with each of these three points:

In assessing the relative poverty of the tropical African flora one encounters as a major obstacle a corresponding poverty of reliable statistics! Good (1974: 170) has been bold enough to estimate the total number of species in the tropical African flora at 30,000. Some regional estimates of numbers of species have also been made (Table 1).

On a basis of the approximate expected degree of endemism and of the number of species still to be discovered, Good's estimate is probably not far off the true total. It should not be forgotten that modern critical taxonomy tends to reduce numbers of species as much as or even more than it adds. However, the African flora is still very far from being fully known. Léonard (1975) pointed out that 7,478 new species were described from Africa (including Madagascar) in the 21 years from 1953–1973, nearly one per day!

How do these figures compare with those for other tropical regions of the world?

Richards (1973) quotes figures of 20,000 for the *Flora Malesiana* region and 9,000 for the Malay Peninsula, an area smaller than Ghana, only one of the several component countries of the area of the *Flora of West Tropical Africa*. Good (1974: 170) estimates the total for Brazil as 40,000 and for India, Pakistan and Burma at 20,000, and on a basis of these and other figures considers that the species density for tropical Africa is much lower than for tropical America and regions of tropical Asia. The species density figure is obtained by dividing the area of a given region in square miles into the number of species occurring in that region.

It is also significant to compare the tropical African figures quoted above with those for Madagascar and Southern Africa. The specific richness of both these areas is much greater than for any comparable area of tropical Africa.

The frequency with which species in tropical Africa show wide geographical ranges is familiar to those who have worked on the botany of this region, but it is difficult to obtain statistics. Hepper (1965) analyzing the affinities of the *Flora of West Tropical Africa*, did a sample analysis of 2,000 species (out of a total of just over 7,000). The result showed that more than 80% were endemic to tropical Africa as a whole, 37% to the area of the *Flora of West Tropical Africa*, and 17% were widespread in Africa (including 1–2% reaching Madagascar).

An analysis of 63 accepted species of *Acacia* in the area of the *Flora of Tropical East Africa* (Brenan, 1959) shows 9 to reach Egypt or Asia, 12 to reach

TABLE 1. Regional estimates of numbers of species in tropical and South Africa and Madagascar.

Area of *Flora of Tropical East Africa* (Kenya, Uganda, Tanzania) (Milne-Redhead, 1971; Polhill, 1976)	10–11,000
Area of *Flora Zambesiaca* (Zambia, Rhodesia, Malawi, Mozambique, Botswana) (Exell, 1971)	6,000
Ethiopia and Somalia (Jardin Botanique National de Belgique, 1976)	6,323
Cameroon (Letouzey, 1976)	6,500
Area of *Flora of West Tropical Africa* (Hepper, 1976)	7,072
Zaïre (Léonard, 1971)	10,000
Madagascar (Keraudren-Aymonin, 1976)	8,200
Southern Africa (South Africa, Lesotho, Swaziland, South West Africa and Botswana) (Killick, 1976)	17,000
(Goldblatt, this symposium)	18,532

West Africa, 17 to reach South Africa, and 33 more or less widespread in eastern Africa. White (1965) in a study of the phytogeography of the woodlands of the Sudano-Zambezian Region found 79 out of 426 tree species common to West Africa and Zambia. Numerous similar wide distributions of Sudano-Zambezian and Saharo-Sindian Region species are given in the fine series of maps published by Lebrun (1977). It would be easy to multiply further examples.

The poverty in or complete absence from tropical Africa of many plant groups, which from their distribution elsewhere might be expected to be well represented in Africa, is striking. There are certain families, for example, which might well be expected but which are quite absent, notably Magnoliaceae, Fagaceae, and Symplocaceae. A fuller discussion will be found in Aubréville (1955). Some examples follow, from Brenan (1954), of families much more poorly represented than they should be:

Theaceae. 3 genera in tropical Africa, 2 of them endemic. Far better represented, both in numbers of genera and species, in Asia and America. *Ternstroemia*, for example, has 2 out of 100 species in Africa.

Myrtaceae. Very richly represented in Asia and America. In tropical Africa only 2 nonendemic genera. *Eugenia* has about 1,000 species of which probably not more than 50–60 occur in Africa.

Melastomataceae. Much more numerous in Asia and especially America than in Africa.

Araliaceae. 2–3 genera in tropical Africa, out of 55. Much more numerous in America and Asia.

Monimiaceae. 1 genus in tropical Africa out of about 20.

Lauraceae. One of the large tropical families with 32 genera and 2,000–2,500 species, mainly in Asia and Brazil. In tropical Africa 5 genera and perhaps 50 species.

Palmae. Moore (1973) gives instructive figures:

Africa, Europe, Arabia	17 genera,	117 species
Madagascar, Mascarene Islands, Seychelles	29 genera,	132 species
South America	64 genera,	837 species
Eastern Tropics	97 genera,	1,385 species

It is noteworthy that palms, often thought of as almost "indicator plants" of the tropics, are by no means rare in Africa except perhaps in rain forest. Their frequency is due to large numbers of individuals of few species. This goes with some very wide distributions in tropical Africa, e.g., *Phoenix reclinata* (Senegal and Kenya to South Africa), *Hyphaene thebaica* (Senegal to Arabia), *Borassus aethiopum* (widely spread), *Calamus deërratus*, etc. The paucity of genera and species is certainly not due to lack of suitable habitats now.

Other examples of families and genera unexpectedly poorly represented in Africa would not be hard to find. Aubréville (1955) mentions the genus *Weinmannia*, only found in Madagascar as far as Africa is concerned but well represented elsewhere. It is relevant that African poverty is not confined to plants. Amadon (1973) made a comparison between the avifaunas of the Congo and Amazon forests and concluded that bird diversity in the Congo forest is at any one locality usually well below that of Amazonia.

What are the reasons for this biotic poverty in tropical Africa? The problem has been discussed by Raven & Axelrod (1974: 607–608) who bring together various likely factors:

(1) Past elimination of taxa by drought.

(2) Major increases in altitude, particularly since the Miocene, accompanied by a cooler and drier climate.

(3) The development of the cold Benguella Current, bringing a drier climate to the West African coast.

(4) Major fluctuations in Quaternary climate, causing corresponding fluctuations in forest areas.

The rich present flora of Madagascar may on this basis be regarded as relict, representing a degree of richness probably shared by much of continental Africa before the violent changes mentioned above took effect. In this way the relative richness of the Indian Ocean islands in, e.g., Palmae is explicable, as also the remarkable links between Madagascar and East Africa with America, e.g., Trigoniaceae, *Rheedia*, *Oplonia*, and the remarkable *Hymenaea-Trachylobium* link discussed by Langenheim (1973).

In this way too the wide disjunctions both at the generic and specific levels between East and West Africa become explicable. For example, the genus *Coleotrype* with one species in West Africa, Zaïre and Uganda, a second in Mozambique and Natal, and others in Madagascar; and the extraordinarily discontinuous distribution of *Mansonia* (Chatterjee & Brenan, 1950), with gaps between Cameroon and Tanzania, and between Tanzania and Assam and Burma (Fig. 1).

After many years' work on the flora of tropical Africa, I am left most strongly with the impression that drastic climatic changes in the past are the only means of explaining distributions that by their discontinuity and unpredictability are a constant warning against the over hasty formulation of theories to explain them!

Phytogeographical Regions of Africa

As knowledge has increased about the distribution within the tropics of Africa of plant species and the types of vegetation they compose, various at-

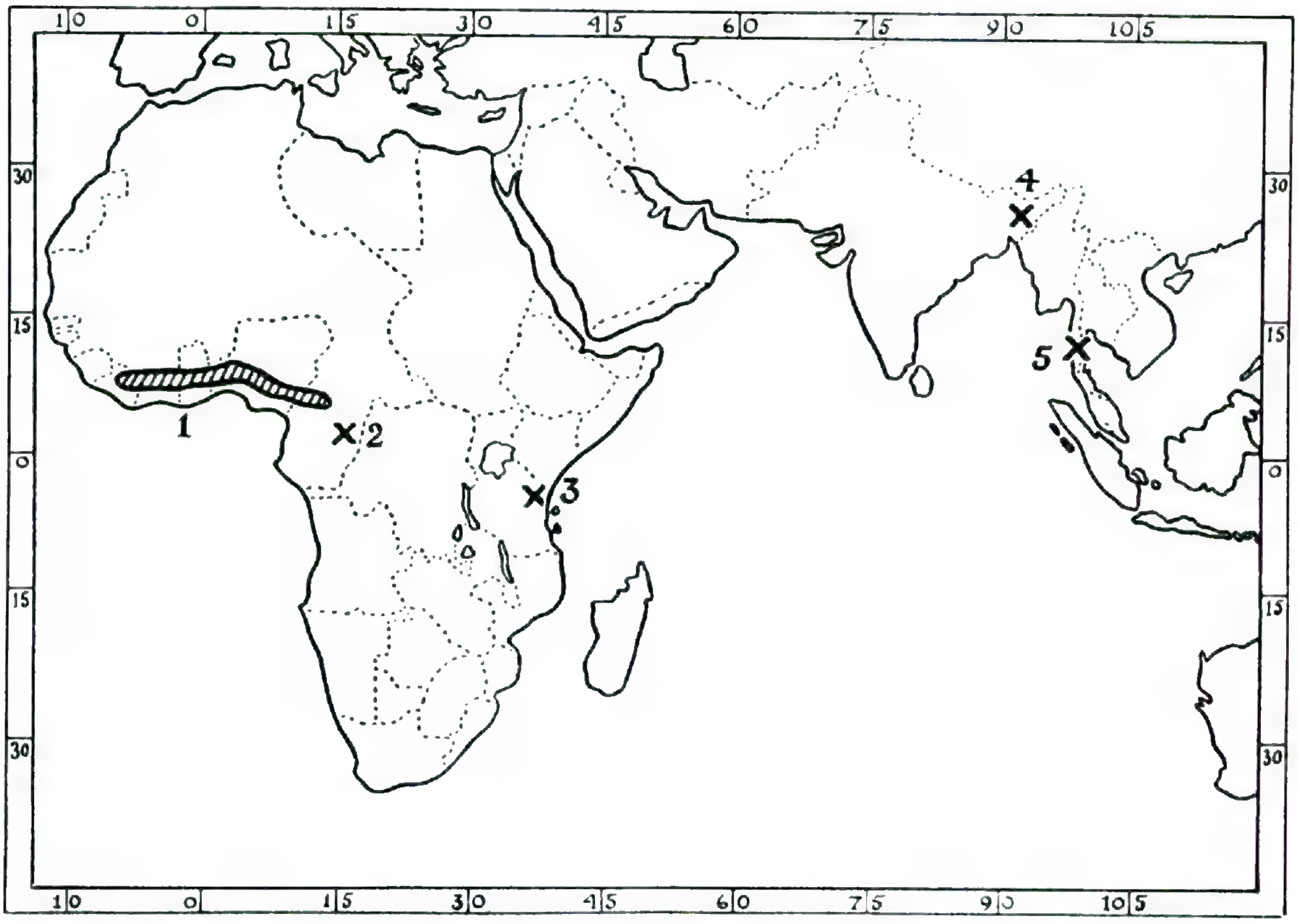


FIGURE 1. Afro-Asian disjunction. Distribution of the genus *Mansonia* (Sterculiaceae): 1. *M. altissima*.—2. *M. nymphaeifolia*.—3. *M. diatomanthera*.—4. *M. dipikae*.—5. *M. gagei*. (After Chatterjee & Brenan, 1950.)

tempts have been made to define phytogeographical regions within tropical Africa and to arrange them schematically. It is not necessary to describe and discuss these schemes in detail here. A recent summary has been given by Schnell (1976: vol. 3: 47–60). Although Good (1974) in his excellent book on the geography of flowering plants divided Africa, with the rest of the world, into floristic regions, his scheme has been justly criticized by Schnell (1976: vol. 3: 58) on the grounds that it takes too little account of the general ecology and fails to give due prominence to disjunct regions linked with higher altitudes.

One of the most recent schemes, and the one accepted here, is set out by Wickens (1976: 40–48), but as he states, it is itself based on two earlier works (White, 1965; Chapman & White, 1970).

Wickens, dealing with the whole of Africa, recognized nine regions, of which five are represented in the area dealt with here. Three of the regions are themselves subdivided into domains (Figs. 2, 3). A brief summary of the regions and domains may be helpful.

1. SUDANO-ZAMBEZIAN REGION

This region corresponds to the tropical savanna and is by far the largest in tropical Africa, extending both north and south of the equator, but physically continuous only by a comparatively narrow isthmus in east Africa.

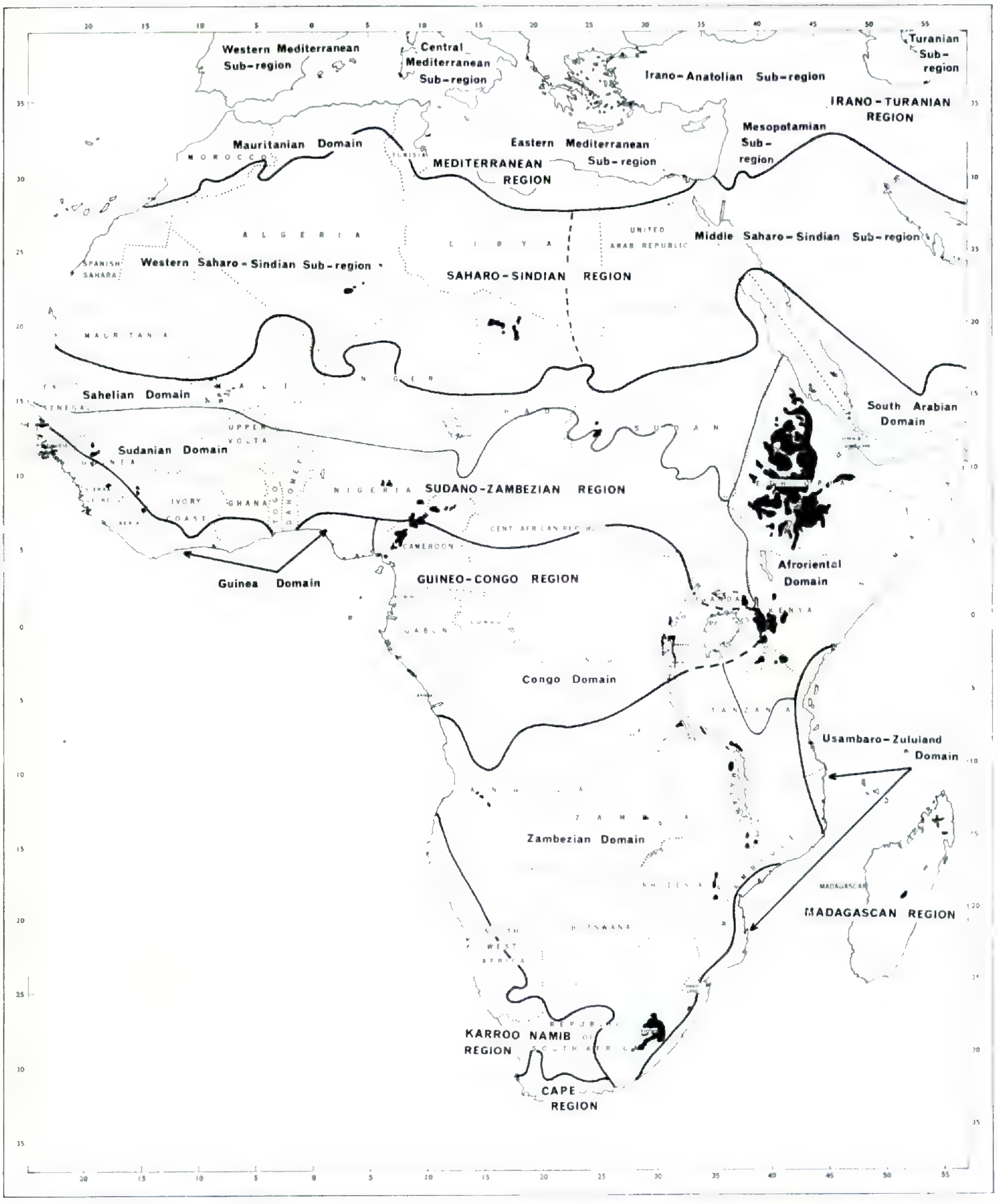


FIGURE 2. Phytogeographical regions and domains of Africa. (After Wickens, 1976.)

To the north it is bounded by the deserts or semideserts of the Saharo-Sindian Region (No. 5). In its central part it embraces towards the west the great forest area of the Guineo-Congo Region (No. 2). To the south it is bounded by South West Africa and South Africa (the Karroo-Namib and Cape Regions, not discussed here).

The region is characterized by a strongly seasonal climate reflected in a range of vegetation types from poor thorn scrub to quite rich deciduous woodland. There are very few endemic families. Although Wickens (1976: 40)

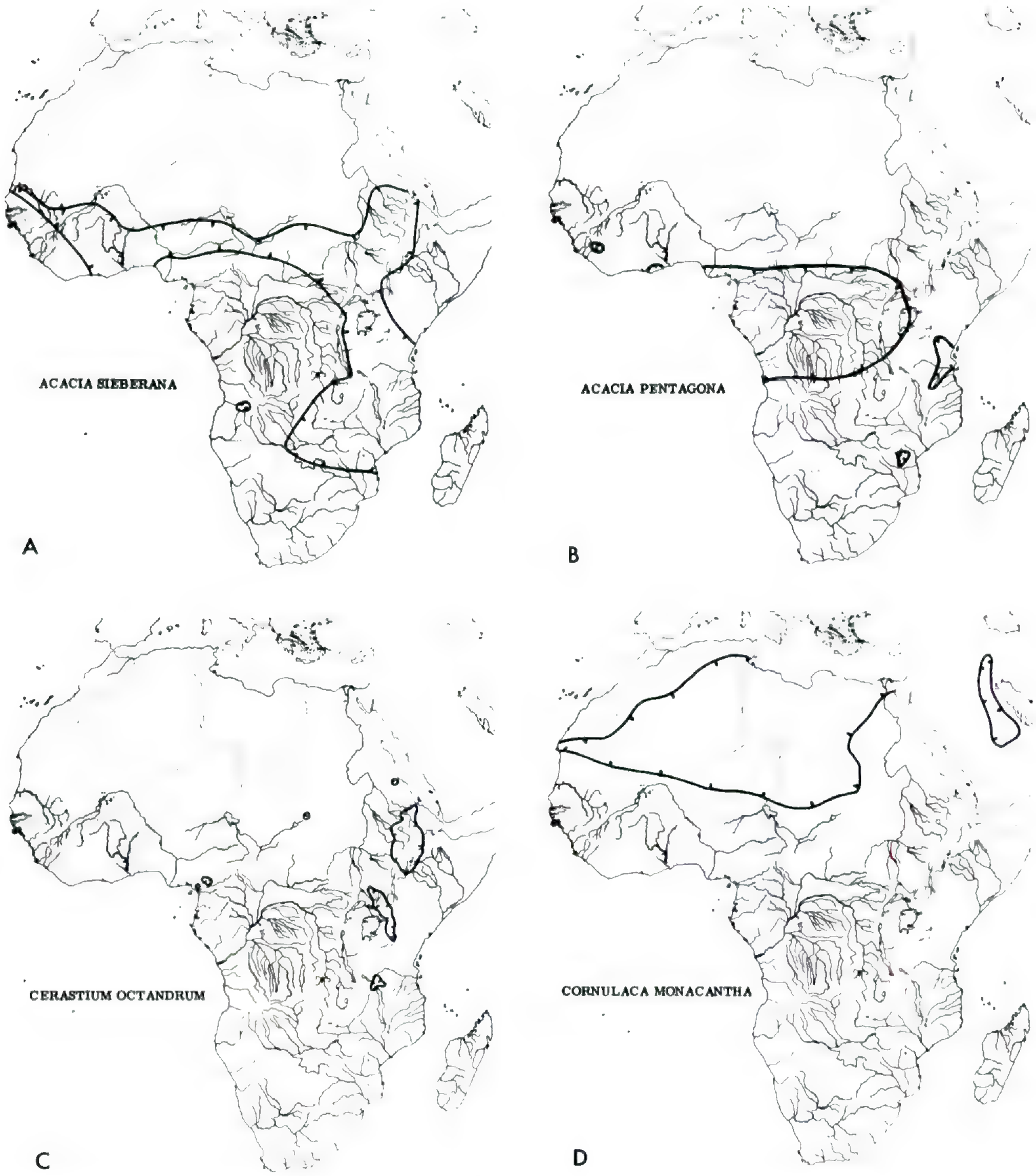


FIGURE 3. Diagrams of some representative distribution patterns of tropical African plant species.—A. *Acacia sieberana* of the Sudano-Zambezian Region; note outlying area in Angola.—B. *Acacia pentagona*, mainly in the Guineo-Congo Region, but also occurring in forest outliers elsewhere. C. *Cerastium octandrum* of the Afromontane Region, showing typical disjunctions corresponding to mountain areas.—D. *Cornulaca monacantha* of the Saharo-Sindian Region, with typical extensions to Arabia and eastwards. (A & C after Wickens, 1976, D after Lebrun, 1977.)

implies that there are few endemic genera, the evidence indicates that this may not be true. It is certain that there are a large number of endemic species and that some genera (e.g., *Crotalaria*, *Indigofera*) have speciated profusely. Some of the more characteristic genera will be mentioned under the component domains, using many of those cited by Wickens (1976). The flora of the region as a whole is discussed more fully on pp. 456–459.

(a) Sahelian Domain.—From Mauritania and Senegal on the Atlantic to the Red Sea coast of the Sudan Republic, forming a belt bounded on the north by the Indo-Turanian Region. Certain widespread species of *Acacia*, *A. senegal*, *A. seyal*, and *A. nubica*, are characteristic, as is the absence of *Terminalia*. White (1965: 657) remarks that it does not have a *distinctive* woody flora and that in West Africa there are only eight tree species which do not also occur in adjacent vegetation zones to the south, and that all eight are extensively distributed in the Oriental Domain (here called Afroriental).

(b) Sudanian Domain.—From Senegal to the Sudan Republic (Ethiopian frontier). This domain forms a rather wider belt than the last, by which it is bordered to the north; to the south it passes into the Guineo-Congo Region. White (1965: 662) states that most woody species of this domain have wide distributions and that there are no well-defined restricted areas of endemism. Characteristic species of this domain are *Isoberlinia doka* and *Khaya senegalensis*.

(c) Afroriental Domain.—In contrast to the Sahelian and Sudanian domains, this area is floristically much richer. Wickens (1976: 41) cites five endemic genera, but this is very far from a complete tally. Certain genera show high speciation, e.g., *Acacia*, *Commiphora*, *Combretum*, the cactiform *Euphorbiae*, *Grewia*, etc.

(d) South Arabian Domain.—Apparently an impoverished extension of the Afroriental Domain, extending into southwestern and southern Arabia. It is little known, and to be noted but not further discussed here.

(e) Zambezian Domain.—This comprises the remainder of the Sudano-Zambezian Region lying to the south of the Afroriental Domain. It is floristically rich and characterized by such genera as *Brachystegia*, *Julbernardia*, *Isoberlinia*, and *Colophospermum*.

2. GUINEO-CONGO REGION

This region represents the main evergreen or partly evergreen forests of Africa, extending southwards to Angola and eastwards to Ruwenzori. There are a number of endemic families and a high proportion of generic endemism. However, in general prolific speciation is absent.

Three domains are recognized.

(a) Guinea Domain.—Extending along the northern coast of the Gulf of Guinea from Gambia to central Nigeria. Poor in endemism compared with (*b*) the Congo Domain.

(b) Congo Domain.—From eastern Nigeria to Angola and the Congo. The richest area in endemism.

(*c*) *Usambara-Zululand Domain.*—The scattered relics of rain forest along or near the eastern coast of Africa, extending from southern Kenya southwards into South Africa. This is the most distinct of the three domains, now very limited in area, but with a high degree of specific endemism, becoming gradually impoverished southwards.

It is proposed to discuss the relationships of the forest flora of tropical Africa in a separate section (pp. 451–456).

3. AFROMONTANE REGION

This region corresponds to the Montane Forest and Ericaceous belts of the tropical African mountain regions. As one might expect, and as can be seen from the map, this region is widespread and notably disjunct, with strong concentrations in eastern Africa, but dispersed elsewhere southwards to Malawi and westwards to Cameroon and other parts of West Africa.

Characteristic species are: *Juniperus procera*, *Podocarpus milanjianus*, *Olea africana*, *Prunus africana*, *Hagenia abyssinica*, and *Hypericum lanceolatum* in the montane forest; species of *Philippia*, *Erica*, *Stoebe kilimandscharica*, and *Adenocarpus mannii* in the ericaceous zone. Although widespread, this region is not floristically rich and is floristically strikingly uniform.

No general analysis of the tropical African montane flora has been published. Morton (1972) analyzed the West African montane flora. Of 718 montane species, 47% are West African endemics, and 53% occur also elsewhere, especially on the mountains of East and central Africa. The latter are thus nearly all strikingly disjunct in distribution, a general feature of the flora of the African mountains. Ayodele Cole (1974) gives some useful lists of endemics. A general discussion of the montane forest plants of Africa is given by Hamilton (1976).

4. AFROALPINE REGION

This is the zone above the Ericaceous belt of the Afromontane Region. It is characterized by giant *Senecio* species, giant *Lobelia* species, low shrubby species of *Alchemilla*, and tufted grassland. It is floristically poor, though with visually striking components, and is strongly endemic, particularly at the species level.

It is almost confined to the high mountains of eastern Africa, from Ethiopia to Tanzania. Although the Cameroon Mountain, for example, is high enough probably to suggest an Afroalpine belt, there is no indication of its development there.

A systematic analysis of the species inhabiting the Afroalpine Region was given by Hedberg (1957). Later refinements (Hedberg, 1965, 1969) resulted in a total of only 278 species, which he analyzed according to their phytogeographical *affinities*. However, no less than 81% of the total are endemic to the high mountains of East Africa. The flora appears to be ancient and of very mixed derivation, both local and distant, from the Cape to Europe and the Himalayas.

Clayton (1976) analyzed the chorology of African montane grasses and found the maximum concentration of single-station endemics (6) in Ethiopia, with surprisingly few elsewhere. A radial movement of species from an Ethiopian reservoir was suggested. Certainly the linkages between ecologically isolated mountains are clear, and even with the geographically remote Cameroon Mountain.

5. SAHARO-SINDIAN REGION

This region of desert and semidesert, extending from Morocco to India, is barely represented in tropical Africa except along the northernmost fringe of

the area. The climate is harsh, with high but often extremely fluctuating temperatures, and low erratic rainfall. The flora is poor and scanty. Wickens (1976: 46) estimates it as only about 1,500 species in all. Endemism is low, indeed almost nonexistent at the family level. Characteristic species include *Calotropis procera*, *Salvadora persica*, *Panicum turgidum*, etc.

Analysis of Endemism and Geographical Affinities of Families

In order to analyze the endemism and geographical affinities of the flowering plant families of tropical Africa, a survey was made, using as a basis Willis's (1973) well-known *Dictionary*, ed. 8. Although some may maintain that the family limits have been defined rather narrowly, nevertheless for the present purpose this has certain advantages, and the work as a whole is valuable as a recent recension of families as critically viewed by a single taxonomist.

Let us first review those families endemic to continental tropical Africa. There are nine: Barbeyaceae, Dioncophyllaceae, Hoplestigmataceae, Huaceae, Medusandraceae, Napoleonaeaceae, Octoknemaceae, Pentadiplandraceae, and Scytopetalaceae.

All the above are strictly endemic, except that Barbeyaceae just reaches adjacent Arabia, though otherwise confined to northeastern tropical Africa—a region well known to be a center of endemism of genera and species.

All the other eight are nearly or quite restricted to the Guineo-Congo Region of tropical Africa and are predominantly inhabitants of the rain forest. Napoleonaeaceae (sometimes considered as part of Lecythidaceae) is entirely a forest family, except for *Napoleona gossweileri*, a tiny suffrutex of the Kalahari Sand savanna in Angola and Zambia—surely an adapted relic and a pointer to drastic climatic changes in the past.

The families are all quite small, the largest being Scytopetalaceae and Napoleonaeaceae, with 5 genera and 20 species, and 2 genera and 18 species respectively. Perhaps this again is indicative of the low level of speciation already noted in the Guineo-Congo Region.

It is instructive to widen the survey of families to cover those occurring in tropical Africa, but restricted to the continent as a whole. Four additional families occur both in tropical and South Africa, but not elsewhere: Kirkiaceae, Melianthaceae, Oliniaceae, and Wellstediaceae.

Of these families only Melianthaceae occurs in West Africa where it is represented by the genus *Bersama*, a taxonomically difficult genus still apparently actively evolving and probably a recent element in the rain forest. The others are represented in eastern tropical Africa, with the Wellstediaceae disjunct between southwestern and northeastern Africa, where it extends to Socotra.

Certain families are restricted to Africa and Madagascar:

Androstachyaceae	:	S.E. tropical Africa (extending to Natal) and Madagascar
Montiniaceae	:	E. tropical and S.W. Africa and Madagascar
Myrothamnaceae	:	E. tropical, South Africa and Madagascar
Ptaeroxylaceae	:	E. and S. tropical, South Africa, and Madagascar

Uapacaceae	:	Tropical Africa and Madagascar
Hydrostachyaceae	:	Tropical and South Africa and Madagascar

All the families so far discussed are small. The largest are Uapacaceae and Hydrostachyaceae, each with 1 genus with 50 and 30 species respectively. Of the six families endemic to Africa and Madagascar all occur in East Africa, and only one, Uapacaceae, occurs in West Africa, but in Guinea savanna, not rain forest.

These distributions emphasize the separation of the West African rain-forest flora from both South Africa and Madagascar. *Cola* (Sterculiaceae), perhaps the largest mainly rain-forest genus in tropical Africa with 125–150 species, is absent from Madagascar. Conversely there is positive evidence of closer links at the family level between Madagascar and East Africa.

Using again the evidence of Willis (1973) there are 14 families endemic to South Africa and 13 to Madagascar. Both groups are thus considerably larger than the group of families endemic to tropical Africa, and underline the richness of the flora of these two regions, or perhaps rather the poverty of the tropical African flora.

It is instructive to broaden the picture to include families restricted to Africa and either America or Asia. Twelve families are African/American and nine African/Asian. At the family level there is no great discrepancy between these two groups; at the generic level there emphatically is.

It is instructive to tabulate these results together and compare them with some derived from other parts of the world as in Table 2.

Analysis of Endemism and Geographical Affinities of Genera

As careful data on geographical distribution are given for each genus in Willis's (1973) *Dictionary of the Flowering Plants and Ferns*, ed. 8, I did a survey of all tropical African genera, using the information in that work supplemented by personal knowledge. This gave the following results: a total of the genera occurring in tropical Africa; a total of the genera endemic to tropical Africa; genera confined to tropical and South Africa; genera confined to Africa and Madagascar; American/tropical African genera; Asian/tropical African genera; and others. It was possible to subdivide the endemic genera, though far from completely or satisfactorily. In the end it was of course possible to express the results in terms of percentages. It should be noted that the figures relate to flowering plants only: the pteridophytes are excluded. The results are given in Table 3.

These figures are, of course, subject to various sources of error. The concept of genera frequently alters with increasing taxonomic knowledge, and with it, of course, the totals in Table 3 are altered. The geographical analysis has had to be made in very broad terms, to conform to the standard of data available. In particular the subdivisions of the endemic tropical African genera must be treated with caution. Both of the first two groups are likely to be augmented from the third. However, in spite of these cautions, the figures are likely to be sufficiently near the truth to allow various points to be made. The figures given

TABLE 2. Distribution patterns and endemism of angiosperm families restricted to Africa, South America or tropical Asia, or restricted to two of these areas.

Region	Number of Families
Endemic to tropical Africa	9
Confined to tropical and South Africa	4
Confined to tropical Africa and Madagascar (and sometimes South Africa)	6
Endemic to South Africa	14
Endemic to Madagascar and/or Mascarenes	13
Confined to tropical Africa and America	12
Confined to tropical Africa and Asia	9
Endemic to tropical Asia	31
Endemic to South America	34

by Good (1974: 99, 145), although based on different geographical areas not too easy to equate, must clearly be modified. In most instances they appear to be considerable underestimates.

The following points may be made on the basis of Table 3.

(1) Between one-third and one-half of the total genera are endemic to tropical Africa, and this is the single most important element. If those also occurring in South Africa are added, it is seen that nearly 60% of the total are endemic to continental Africa. The uniqueness of the African flora is sufficiently attested.

(2) West and central tropical Africa are richer in endemic genera than the east and south (19.62% against 12.62%). Although the evidence is inadequate for exact analysis, it is likely that the majority of the western and central endemics are forest genera, the generic endemism outside the forest areas of West Africa being small.

(3) The percentages of tropical African genera extending to South Africa and Madagascar (8.81% and 7.05%) are surprisingly low proportions of the total of tropical African genera.

(4) No less than 464 genera (18.59%) extend to Asia and/or Australia. This element is numerically next in size to the tropical African endemic one, and is a clear indication of the importance of the phytogeographical links between Africa and Asia.

(5) Conversely, the tropical African/American element is small (88 genera—3.52%).

(6) The relative significance of the pantropical and temperate elements is noteworthy.

It may be instructive to compare the figures given in Table 3 to those in Table 4 giving some parallel percentages obtained from a separate study of the geographical relationships of the genera of Leguminosae occurring in tropical Africa (Brenan, 1965).

The similarity between the proportions in Table 4 and those in Table 3 are striking. The tropical African-Madagascan element is considerably less, and the pantropical more, the latter perhaps reflecting the weediness and wide distributions of a number of genera in the Papilionioideae.

TABLE 3. Distribution patterns of tropical African genera. Total number of genera occurring in tropical Africa: 2,497 (100%).

Region	Total Genera	Percentage	
Endemic to tropical Africa	1,081	43.33	
W. and central tropical Africa	490	19.62	
E. and S. tropical Africa	315	12.62	
General or unspecified	276	11.05	
Endemic to tropical and South Africa	220	8.81	15.86
Endemic to tropical Africa and Madagascar (with sometimes South Africa)	176	7.05	
Restricted to tropical Africa and Asia (plus sometimes South Africa)	351	14.06	18.59
Restricted to tropical Africa, Asia and Australia or tropical Africa and Australia alone	113	4.53	
Restricted to tropical Africa and America	88	3.52	
Pantropical	303	12.13	
Mainly temperate but occurring in tropical Africa	148	5.92	

This is perhaps a convenient place to discuss more fully the relative importance of the links with America and Africa. The analysis of family distributions (Table 2) shows that at this level there is little significant difference numerically between the two elements, but at the generic level the balance is very strongly weighted in favor of Asia. Thorne (1973) has analyzed the floristic relationships between Africa and tropical America and has carefully tabulated the families and genera in common. His total of 111 African/American genera is higher than the 88 given here, because he takes Africa in a wide sense, including South Africa, Madagascar, and the Mascarenes. As Thorne states, the floristic links between tropical Africa and tropical America are undeniable, and some are spectacular (Fig. 4). The occurrence in Africa of *Pitcairnia feliciana* (Bromeliaceae), *Kissenia* (Loasaceae), *Erismadelphus* (Vochysiaceae), *Maschalocephalus* (Rapateaceae), *Sacoglottis* (Humiriaceae), *Mayaca baumii* (Mayacaceae), *Cylicomorpha* (Caricaceae), etc., have attracted wide and justified attention. However, Thorne draws attention, quite justly, to the absences as well as the presences, and tabulates (p. 35) a considerable number of large or very large African and American genera which might have been expected to occur in both continents, but do not. As he says, this is a factor which must be consid-

TABLE 4. Distribution patterns and proportions of genera of Leguminosae occurring in tropical Africa. Total number of genera: 229.

Region	Total Genera	Percentage
Endemic to tropical Africa	96	41.92
Endemic to tropical and South Africa	16	6.99
Endemic to tropical Africa and Madagascar	4	1.74
Restricted to tropical Africa and Asia and/or Australia	35	15.28
Restricted to tropical Africa and America	10	4.37
Pantropical	42	18.34
Mainly temperate or Mediterranean but occurring in tropical Africa	14	6.11

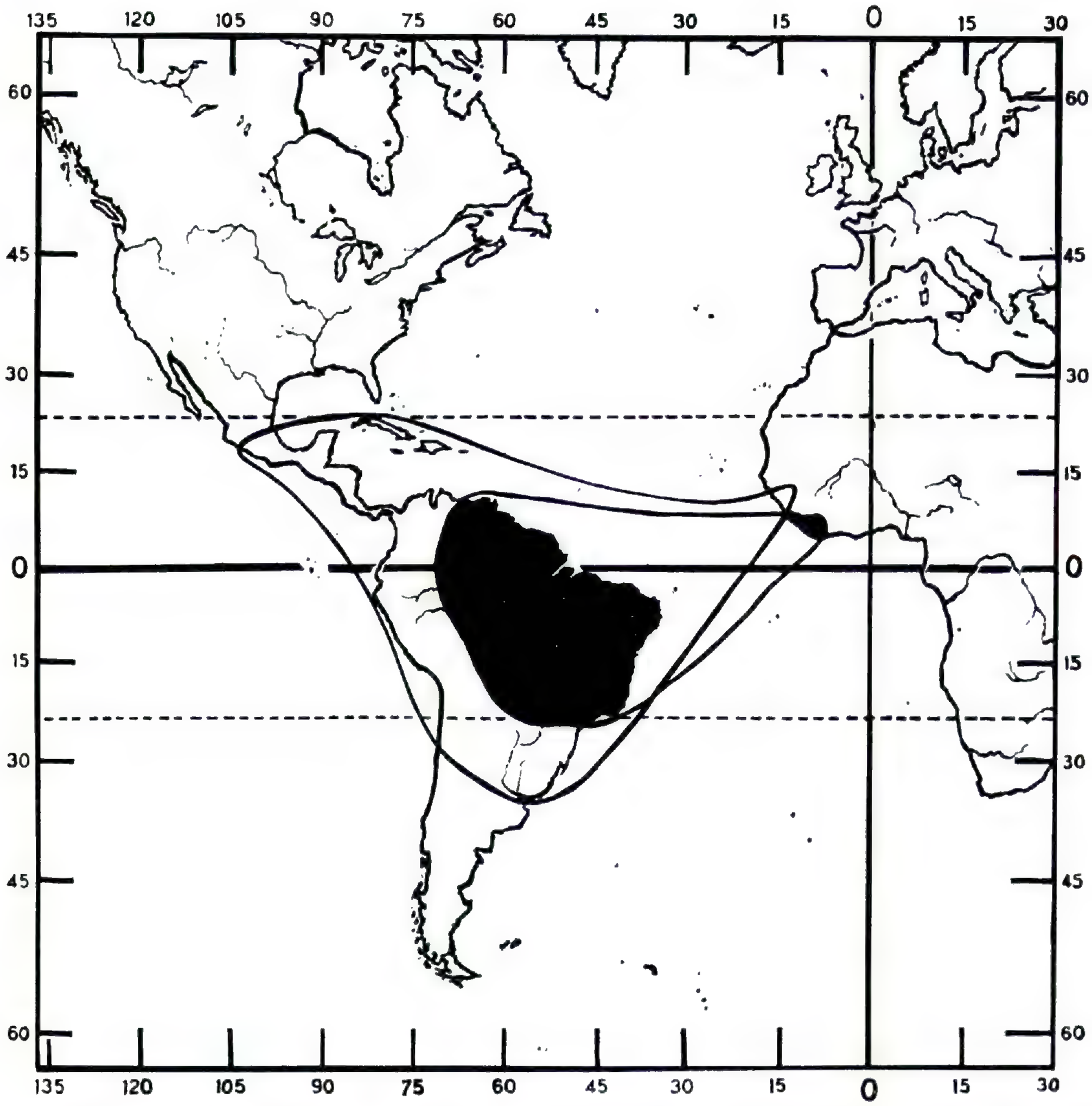


FIGURE 4. Afro-American disjunctions. Distribution of Bromeliaceae (white area) and of Rapateaceae (black area). The only African members of these families are *Pitcairnia feliciana* and *Maschalocephalus dinklagei* respectively. (After Hepper, 1965.)

ered. He concludes that a comparison of the floristic links between tropical Africa, tropical America, and Asia would appear to rule out continental drift as a valid explanation of these widely disjunct ranges, and I agree with him that long-distance dispersal would seem quite adequate to explain the floristic relationships between tropical Africa and tropical America. A similar conclusion was reached by Ayensu (1973), in considering the remarkable Afro-American family Velloziaceae with 47 species in Africa, 3 in Madagascar and about 200 in South America.

ENDEMISM IN THE TROPICAL AFRICAN RAIN FOREST

In 1954 I carried out a detailed study of endemism in the rain forest areas of tropical Africa (Brenan, 1954). Since most of this has not been published and in spite of the lapse of time, the conclusions still seem relevant and valid, some

TABLE 5. Area subdivisions of the tropical African rain forest. Areas numbered; area-groups indicated by letters.

A. Western: Sierra Leone-Ghana
    1. Sierra Leone
    2. Liberia
    3. Ivory Coast
    4. Ghana
B. West and central Nigeria
    5. Nigeria (west and central)
C. Cameroon, Gabon and Congo-Brazzaville
    6. Nigeria (eastern)
    7. Cameroon (northwestern) and Fernando Po (Macías Nguema)
    8. Cameroon (remainder) and Principe
    9. Gabon, Equatorial Guinea, São Tomé, Annobon
    10. Cabinda
    11. Congo-Brazzaville
D. Zaïre
    12. Zaïre
E. Uganda
    13. Uganda
F. Tanzania
    14. Usambaras
    15. Ngurus and Ulugurus
G. Northern Forest Outliers (Republic of Guinea to Sudan Republic)
H. Southern Forest Outliers (Angola eastwards to Zambia and Rhodesia)
I. Eastern Forest Outliers [Kenya, Tanzania (except as under F), and Mozambique]

of the main ones are described here. The analysis was based entirely on a personal examination of herbarium material at the Royal Botanic Gardens, Kew, supplemented by field experience in East and West Africa.

The rain forest area was taken in its widest sense, to include not only the main block in West and central Africa, but also the easterly extension into Uganda, the outlying island areas in Tanzania, and the other outlying areas from the Republic of Guinea to the Sudan and southwards to Rhodesia and Mozambique.

The area subdivisions, updated nomenclaturally, are listed in Table 5.

It will be seen that the total region defined corresponds (except for various outliers) roughly to the Guineo-Congo Region, including the Usambara-Zululand Domain.

Let us now discuss the results. Of 133 families present, 8 (6.01%) are endemic to the rain forest areas as defined. Of a total of 1,121 genera, 492 (43.9%) are endemic to the rain forest region and 629 (56.1%) nonendemic. Among the nonendemic families, the degree of generic endemism varies from 0–100%. Among larger families or subfamilies with high proportions of endemism are the following:

Myristicaceae	5 genera	100%
Sapotaceae	26 genera	83.9%
Annonaceae	25 genera	73.2%
Melastomataceae	16 genera	72.7%
Leguminosae—Caesalpinioideae	41 genera	67.8%
Apocynaceae	24 genera	61.5%

TABLE 6. Numbers and proportions of genera endemic to the tropical African rain forest occurring in single-numbered areas, or area-groups G, H, and I as defined in Table 5.

Area	Number of Endemic Genera	Proportion of Total Generic Endemism in Each Area
1. (Sierra Leone)	1	0.6
2. (Liberia)	1	0.7
3. (Ivory Coast)	5	3.9
4. (Ghana)	2	1.25
5. (Nigeria, N., W. and C.)	1	0.6
6. (Nigeria, E.)	4	2.1
7. (Cameroon, N.W. and Fernando Po)	5	2.5
8. (Cameroon, remainder and Principe)	26	8.9
9. (Gabon, Equatorial Guinea, and islands)	28	9.5
10. (Cabinda)	1	0.6
11. (Congo-Brazzaville)	3	5.8
12. (Zaïre)	19	7.9
13. (Uganda)	0	0
14. (Usambaras)	4	7.7
15. (Ngurus, Ulugurus)	7	25.9
G.	4	3.6
H.	7	7.1
I.	2	3.0

It should be noted that the above analysis of Sapotaceae was made at a time when generic fragmentation in the family had not reached its present-day state. Probably now both the number of genera and the proportion of endemism would be higher. It is also noteworthy that none of these larger families is represented by an outstandingly large number of endemic genera—another facet of the floristic poverty of tropical Africa referred to elsewhere. Taking only those families possessing some proportion of endemism among their genera, the average of endemism per family is 55.12%.

An analysis of the numbers of genera in single-numbered areas and area-groups G, H, and I (see Table 5) is given in Table 6.

It can be seen from these figures that areas 1–4 are collectively rather poor in endemic genera, these possessing large rain forest areas. The contrast between the two parts of Nigeria, areas 5 and 6, is noteworthy and is decidedly confirmed by field experience. There is clearly a phytogeographical discontinuity here, located somewhere between the Niger and Cross rivers. The relative richness in endemic genera shown in Cameroon and Gabon emerges very clearly from the above table. In each area the number of endemic genera is much greater than that of Zaïre, in spite of the much more extensive rain forest in Zaïre. This contrast is surely attributable to the effect of past climatic changes; see Chapin (1936).

Passing to East Africa, the absence of any endemic genus in Uganda is interesting in comparison with Tanzania, and suggests that the rain forest in Uganda is no more than a depauperate eastward extension of the rain forest of eastern Zaïre. The generic endemism of the Usambaras, Ulugurus, and Ngurus in Tanzania is striking.

TABLE 7. Analysis of endemic tropical African rain forest genera occurring in 3 or more area-groups as defined in Table 5.

Area Groups	Number of Endemic Genera	Proportion of Total of Endemic Genera
1) ABC	27	5.49
2) ABCD	54	10.97
3) ABCDE	34	6.9
4) ABCDEF	17	3.45
5) BCD	10	2.04
6) BCDE	3	0.61
7) CDE	17	3.45
8) CDEF	6	1.22

An analysis was made of genera occurring in three or more area-groups (see Table 5) and this is instructive (Table 7). Discontinuities, which are striking, will be discussed separately below.

Out of a total of 492 endemic genera, 167 or 33.94% have widespread ranges, in the sense adopted above. The rather high number of genera in (1), which fail to reach Zaïre, is notable (Table 7). If the total numbers of widespread endemic genera are taken for each area-group, the following figures are obtained: A—144, B—145, C—168, D—141, E—82, F—32.

In each of the areas A–D, the totals are roughly similar, with C slightly higher than the rest. This is in very marked contrast to the figures given in Table 6 of narrowly endemic genera restricted to numbered areas, where area-groups C and to a lesser extent D are very much richer in narrowly endemic genera than other area-groups. This contrast is hard to explain. It may be that these widespread genera represent the ancient core of a widespread tropical African rain forest flora, which has in the course of time given rise to the narrowly endemic genera. On the other hand, these widespread genera may have attained their ranges more recently, through such means as effective long-distance dispersal or abundant seed production. Both causes may well have had their effect, though I suspect that the second may have been more significant than the first. The prevalence of wind-dispersed emergent trees in the Nigerian rain forest is significant, and also the importance of clearings in their regeneration.

Mention has already been made of the discontinuities in distribution that are a feature of the rain forest flora of tropical Africa. The analysis given in Table 8 was made.

The first group, found in the area Sierra Leone-Ghana but absent from western and central Nigeria, but appearing again in eastern Nigeria or other countries to the south, is a large one with 73 genera. This discontinuity is also found at the specific level: e.g., *Cola chlamydantha*, *Protomegabaria macrophylla*, *Thecacoris stenopetala*, *Pararistolochia mannii*, etc. Similar examples among mammals are given by Rosevear (1953: 35). This discontinuity is discussed by Guillaumet (1967: 145–168) and corresponds to Groups IV and V of his "espèces Sassandriennes," with 47 species discontinuous between the Ivory Coast or Ghana and the Cameroon-Congo area. On this evidence Guillaumet

TABLE 8. Discontinuities between area-groups as defined in Table 5 shown by genera endemic to the tropical African rain forest.

Discontinuity	Number of Genera Involved	Percentage of Total of Endemic Genera
1. Between A and C (absent from B)	73	14.63
2. Between A and D	3	0.61
3. Between A and E	1	0.20
4. Between A and F	1	0.20
5. Between A and I	1	0.20
6. Between C and E	12	2.43
7. Between C and F	9	1.83
8. Between C and H	2	0.41
9. Between C and I	10	2.04
10. Between D and F	10	2.04
11. Between D and I	11	2.24

postulates "refugia" of forest in Sierra Leone and Liberia in a past period of arid climate.

Discontinuity 6, involving 12 genera missing from Zaïre, is probably more apparent than real and may well reflect poor knowledge of the Zaïrian rain forest.

The discontinuities between C and F and between D and F are important. Although some may eventually be found in Uganda (E), the latter country is comparatively well-known botanically. The evidence indicates that the rain forest flora in the Usambaras, Ulugurus, and Ngurus in Tanzania has long been isolated, showing affinities with West Africa at the generic rather than the specific level, and was probably derived from a previous rain forest flora in which many of the widespread genera present today in Uganda and Zaïre were absent. The rain forest in F may thus represent the fragmented relics of a primitive and formerly more widespread forest flora not clearly recognizable elsewhere in Africa today. Moreau (1952) suggests that the eastern African lowland rain forests may have been separated from the western at least since the mid-Pleistocene, and possibly a good deal longer—a period of 500,000 years or more.

The presence of endemic species of predominantly rain forest groups in habitats other than rain forest in East Africa is also evidence pointing in the same direction, e.g., *Mansonia diatomanthera* (Chatterjee & Brenan, 1950), *Berlinia orientalis*, and the East African species of *Tessmannia* (Brenan, 1967). There are many other examples.

So far the endemic genera have been treated as units, with little or no reference to their size. An analysis shows that 231 out of the 492 endemic genera are monotypic, 82 have two species each, 48 have three species each, and so on—in general the more species in the genus the fewer the genera become. Thus, at the other end of the scale, there are single genera each with 25, 27, 28, 34 and 36 species; none with more. Thus, none of the genera endemic to the tropical African rain forest region is large. Although some genera in the region may be represented by as many as 100 species, e.g., *Cola*, *Rinorea*, *Psychotria*, and *Ficus*,

none is confined to rain forest, and all except *Cola* are found in other continents than Africa.

THE SAVANNA AND WOODLAND REGIONS OF TROPICAL AFRICA

The savanna and woodland areas of tropical Africa, corresponding in general to the vast Sudano-Zambezian phytogeographical Region (Fig. 2), has unfortunately not been subjected to the same detailed phytogeographical analysis as has the Guineo-Congo rain forest Region. Of necessity, then, any general comments must be tentative and subjective, liable to reexamination when the gradual accumulation of evidence permits. As can be seen from the map (Fig. 2), the continuous tracts of savanna, particularly north of the equator, are far greater than those of any other vegetation type in Africa.

Although it is evident that there has been in the past floristic interchange between the forest and savanna (cf. particularly the presence of species of forest affinity in the savannas of southern Africa, e.g., *Napoleona gossweileri*, *Caloncoba suffruticosa*, *Syzygium huillense*, *Magnistipula eglandulosa*), nevertheless the "violent contrast" between the savanna and forest floras of tropical Africa has been emphasized by Monod (1971: 377).

White (1965) studied the individual distributions of 426 Sudano-Zambezian savanna-woodland tree species. Generic endemism was found to be slight (15%), but specific endemism high within the region, most of the 426 species being endemic, only 2 occurring also in the Guineo-Congo Region. Both at the generic and specific levels the relative richness of the Zambezian Domain within the region emerges. In West Africa there are 171 species, in Zambia 334. Of the Zambian species 34% are confined to three clearly defined centers of endemism, the Katangan, Barotse, and Zambezi. These results for tree species are readily paralleled in other life forms.

Although the disjunctions of distribution so obvious in the Guineo-Congo Region have been less publicized in the Sudano-Zambezian Region, they are there and give clear indication of climatic fluctuations and changes in the past as severe as those affecting the rain forest. Lebrun (1971) has given and mapped some remarkable examples of disjunction between the savanna regions of northern and southern tropical Africa. De Winter (1971) has focussed attention on the disjunctions linking the more arid areas of northern and southern Africa. Such disjunctions, although remarkable, emphasize the basic unity of the Sudano-Zambezian Region. Remarkable examples of such distributional discontinuities as *Kissenia* (South West Africa, Somalia, and Arabia) and *Wellstedia* (South West Africa, Socotra, and northeastern Africa), at first sight quite anomalous, fall into place against a background of numerous discontinuities, many of them less extreme and passing into examples of more continuous distribution.

Gillett (1958) revised the genus *Indigofera* in tropical Africa. This genus is represented in the Sudano-Zambezian Region of tropical Africa by numerous species, in excess of 250, is widespread, and barely penetrates the forest areas. Gillett set out the geography in some detail, and it therefore seemed appropriate and useful to analyze its distribution (Table 9) in terms of its occurrence in the various domains of the Sudano-Zambezian Region, to make an assessment of its

TABLE 9. Analysis of distribution patterns of African species of *Indigofera*, using data from Gillett (1958). Total number of species: 279.

Region			Number of Species
Non-African (or occurring only outside continental Africa)			5
Occurring in more than one region and not analyzed further			29
Confined to Guineo-Congo Region			2
Confined to Karroo-Namib Region			9
Confined to Sudano-Zambezian Region + Usambara-Zululand Domain			232
Region doubtful			2
Sudano-Zambezian Region (232)			
In more than one Domain			83
N. and S. of Equator		44	
N. of Equator		13	
S. of Equator		26	
In Sahelian Domain only			2
In Sudanian Domain only			30
Narrow endemics:			
Guinea Republic		3	
Nigeria		3	
Sudan Republic		1	
Central African Republic		2	
In Afroriental Domain only			45[a]
Narrow endemics:			
Ethiopia		5	
Somalia		5	
Socotra		2	
Kenya		5	
Tanzania		12	
In Usambaro-Zululand Domain only			17
Narrow endemics:			
Tanzania		1	
Mozambique		6	
In Zambezian Domain only			55
Narrow endemics:			
Zaïre		3	
Mozambique		1	
Zambia		3	
Rhodesia		1	
Angola		8	
Transvaal		2	

[a] Of the species other than narrow endemics 11 are confined to N. of the Equator, only one to the S. and only one occurring both N. and S.

local endemism, and to compare the savanna areas north and south of the Equator.

A number of significant conclusions emerge from these figures.

(a) The large number of species occurring in more than one domain, and also north and south of the Equator.

(b) The small number of species apparently confined to the Sahelian Domain.

(c) Except in the Afroriental Domain, which is a special case, 45 species are restricted to north of the Equator, and 143 to the south.

(d) North of the Equator (except in the Afroriental Domain) narrow endemism is mainly towards the west (Nigeria and Guinea), but even here the numbers are very low compared with elsewhere in the Region.

(e) In the Afroriental Domain, the high endemism of the "Horn of Africa" emerges clearly. Of the 5 Kenya endemics, 4 are confined to the northeast. The richness of Tanzania is also evident.

(f) In the Zambezian Domain, the endemism is less than one might expect in Zambia, but high in Angola.

Although there are obvious possible sources of error in utilizing the above data (e.g., lapse of time and difficulty in establishing clear boundaries of regions and domains), nevertheless it is unlikely that the general pattern and the deductions drawn will be much altered. Most of the deductions can be readily paralleled by experience of other taxonomic groups in tropical Africa. For example, in the genus *Acacia* there are very few endemics indeed in the Sudanian and Sahelian domains. Although the genus is well represented there, most of the species are more or less widespread in tropical Africa and not infrequently extend into Asia. The "Horn of Africa" has at least a dozen endemic species of *Acacia*, and no other part of Africa shows as many. Secondary areas of concentration occur in Tanzania and in the area Rhodesia-Botswana-Mozambique-northern Transvaal.

Further studies, both general and local, of the phytogeography of the Sudano-Zambezian Region of tropical Africa would be most welcome. However, this region as well as being the largest in Africa is also I suspect considerably more heterogeneous than the rest. It includes a wide range of vegetation types ranging from thorn scrub and grassland to savanna and rich woodland. Furthermore the phytogeographical origins and history of these various vegetation types may be by no means always the same. These differences are not, I think, adequately reflected in the domains composing the Sudano-Zambezian Region. For example, the Afroriental Domain includes the area of northern Kenya-Somalia-Socotra-Ethiopia, in which are to be seen the remains of a highly endemic, probably comparatively ancient flora very different from that of the rest of Kenya and Tanzania, thus raising the question of whether the domain is really a single one or whether it would be better divided.

The variety of vegetation types in the Zambezian Domain is indicated by the works of Wild & Fernandes (1967) and Fanshawe (1969). One of the remarkable features of this domain is the prevalence over huge areas of woodland or savanna woodland in which the genera *Brachystegia* and *Julbernardia* are conspicuous or dominant—the so-called "miombo." Typically this occurs in no other domain. Attempts have been made to parallel "miombo" in West Africa, but at best the differences are profound.

In terms of numbers of woody species, this is the richest vegetation type in Zambia (Fanshawe, 1969: 43), and this richness is particularly evident also in the herb layer. Many of the local endemics so frequent in Zambia, Angola, and southern Zaïre occur in "miombo." A remarkable feature is the richness of suffrutices, often relatives of large trees that have adopted a habit nearer to that of a perennial herb. Carcasson (1964) notes that the "Zambesian Zone," roughly corresponding with the tropical part of the Zambezian Domain, is the richest of the southern areas recognized by him in species of butterfly and that there are numerous endemics.

The "miombo" is linked with a relatively high rainfall (700–1,600 mm per annum) and occurs on a plateau of about 1,000–1,500 m elevation. Fanshawe (1969) reproduces a map showing the hypothetical vegetation of Zambia at a rainfall 500 mm per annum less than at present, entailing a spectacular decrease in the present area of "miombo." Although Fanshawe (1969: 42) states that "miombo" woodland is a "vigorous invasive vegetation type," I have seen in Zambia "miombo" woodland areas closely similar in their tree cover, but very different indeed in their understory of shrubs and herbs. In fact it may be desirable to analyze separately in terms of composition and behavior the tree and understory layers of "miombo" woodland. An invasive tree layer may spread over lower layers floristically and historically different.

The "miombo" stands in strong contrast to the tree savannas in which there is a prevalence of *Acacia* and *Combretum*, well represented in the Zambezian Domain, usually at lower elevations and lower rainfall, but also much more widespread in Africa and recognizably occurring in other regions and domains.

In the Zambezian Domain there are thus vegetation types as floristically distinct and probably also as different in their history and origin as those in the Afroriental Domain. In any analysis or comparison of floras or endemism it is important that these differences are clearly recognized.

Endemism of Areas and Individual Countries

During the course of this study an attempt has been made to assess the relative richness in endemics of individual areas and countries in tropical Africa. The areas correspond with the regional groupings of countries adopted in the herbarium of the Royal Botanic Gardens, Kew, while the countries correspond with the usual political boundaries. The only noteworthy exception is Cameroon. The northwestern part (corresponding to the old British Cameroons) has been completely dealt with in the second edition of the *Flora of West Tropical Africa* (Hutchinson & Dalziel, 1954–1968), while the definitive *Flore du Cameroun* is still very incomplete. It has thus seemed worthwhile to treat these two areas separately, though recognizing that they are politically one. Approximate areas in square kilometers are given after the name of each country. I am greatly indebted for many of the data used in this assessment to the unstinted help of the Conservation Unit at the Royal Botanic Gardens, Kew, especially Mr. G. Ll. Lucas and Mr. John Hartshorne. Mr. Hartshorne in particular has been responsible for most of the detailed and arduous extraction of data from published works, particularly in 10A, 10D, and Zaïre.

WEST AFRICA: AREA OF FLORA OF WEST TROPICAL AFRICA

Analysis of the total of taxa (Hutchinson & Dalziel, 1954–1968), species and varieties being considered as separate taxa, shows the results enumerated in Table 10.

These figures emphasize the regional or more narrow endemism characteristic of so large a proportion of the flora of tropical West Africa. The families with the largest number of taxa endemic to one country (over 25) are as follows:

Rubiaceae—107,
Papilionaceae—52,
Orchidaceae—48,
Melastomataceae—38,
Gramineae—37,
Euphorbiaceae—34,
Compositae—33,
Caesalpiniaceae—31,
Sterculiaceae—27,
Annonaceae—26,
Cyperaceae—25.

In the following account totals of specific endemism are given for each country, i.e., species endemic to that country alone, together with some remarks on areas of special concentration and some representative or outstanding examples. Percentages are given of the total species of the *Flora of West Tropical Africa* (7,072). These will of course be much higher if considered as percentages of the country floras concerned.

Senegal (200,000 km^2).—26 endemic species (0.37%). Examples: *Abutilon macropodum*, *Acalypha senegalensis*, *Berhautia senegalensis*, *Cyperus lateriticus*, *Eriocaulon inundatum*, *Laurembergia villosa*, *Rhynchosia albiflora*, *Salicornia senegalensis*, *S. praecox*, *Vernonia bambilorensis*. Note the absence of forest genera and predominance of herbs. *Berhautia* is apparently an endemic genus. Clayton & Hepper (1974) identify "Senegal/Mali" as a center of endemism for West African grasses.

Gambia (10,700 km^2).—One endemic species, *Rhinopterys spectabilis*.

Guinea-Bissau (36,100 km^2).—Apparently no endemism at the specific level.

Guinea Republic (250,000 km^2).—88 endemic species (1.24%). Examples: *Adamea stenocarpa*, *Cailliella praerupticola*, *Djaloniella ypsilostyla*, *Fleurydora felicis*, *Guyonia tenella*, *Impatiens bennae*, *Pitcairnia feliciana*, *Rinorea djalonensis*, *Stonesia* (3 species). Schnell (1968) has pointed out certain especially important areas: the Nimba Mountains, Fouta Djallon, etc. The Guinea Republic is an important center of endemism: the number of endemic taxa is high, and the genera *Adamea*, *Cailliella*, *Djaloniella*, *Fleurydora*, and *Stonesia* all appear to be endemic. In addition the only African bromeliad, *Pitcairnia feliciana*, occurs in this country. Clayton & Hepper (1974) identify "Guinée/Sierra Leone" as an important center of endemism for West African grasses, although "endemic" is by them equated with "endemic to the area of the *Flora of West Tropical Africa*."

Mali (1,500,000 km^2).—11 endemic species (0.15%). Examples: *Combretum nioroense*, *Gilletiodendron glandulosum*, *Letestuella chevalieri*, *Teclea ferruginea*. In spite of its area Mali is outside the Guineo-Congo Region and is poor in endemism.

Sierra Leone (72,300 km^2).—74 endemic species (1.04%). Examples: *Acioa whytei*, *Afrotrilepis jaegeri*, *Byttneria guineënsis*, *Clerodendrum whitfieldii*, *Dovyalis afzelii*, *Gilbertiodendron aylmeri*, *Habropetalum dawei*, *Paepalanthus pulvinatus*, *Tricalysia trilocularis*. Somewhat less rich than the Guinea Republic, and with apparently only one endemic genus, *Habropetalum*. Ayodele Cole (1974) lists the few endemic species of the Loma Mountains/Tingi Hills in Sierra Leone.

TABLE 10. Endemism in West Africa: area of the *Flora of West Tropical Africa*. Total number of taxa: 7,172.

Region	Number	Percentage of total
Endemic to 1 country	1,001	13.96
Endemic to 2 countries	545	7.6
Endemic to 3 countries	328	4.57
Endemic to more than 3 countries	593	8.27
Endemic to *Flora* area plus 1 adjacent country outside	414	5.77
Occurring more widely	4,290	59.83

Liberia (111,500 km²).—59 endemic species (0.83%). Examples: *Ancistrocladus pachyrhachis, Dichapetalum linderi, Dinklageodoxa scandens, Guibourtia dinklagei, Hymenocardia intermedia, Jasminum dinklagei, Tetracera dinklagei.* The only endemic genus is the remarkable *Dinklageodoxa*, the only scandent member of the Bignoniaceae indigenous to Africa.

Ivory Coast (322,000 km²).—41 endemic species (0.58%). Examples: *Coffea lemblinii, Cola attiensis, Gymnostemon zaizou, Hemandradenia chevalieri, Homalium aubrevillei, Impatiens nzoana, Macaranga beillei, Sapium aubrevillei.* The only endemic genus appears to be *Gymnostemon.* The alleged endemic genus and species, *Vilbouchevitchia atro-purpurea* A. Chev., is highly suspect (see Hutchinson & Dalziel, 1954–1968, vol. 2: 74). Guillaumet (1967) discusses the species endemic to the Ivory Coast and the region Ghana-Sierra Leone ("espèces sassandriennes"). Group I (17 species) is confined to the western Ivory Coast (and often Liberia); Group II (75 species) to the region Ivory Coast–Sierra Leone.

Ghana (238,300 km²).—43 endemic species (0.61%). Examples: *Afrothismia pachyantha, Aneilema mortonii, Cola umbratilis, Homalium angustistipulatum, Millettia irvinei, Ochthocosmus chippii, Talbotiella gentii.* Apparently no endemic genera.

Togo (56,000 km²).—20 endemic species (0.28%). Examples: *Adenia triloba, A. pulcherrima, Eugenia togoensis, Gutenbergia foliosa, Jaundea baumannii, Rinorea bussei, Streptocarpus kerstingii.* No endemic genera.

Dahomey (112,600 km²).—11 endemic species (0.15%). Examples: *Hibiscus lonchosepalus, Jatropha atacorensis, Lepidagathis chevalieri, Polygala atacorensis, Raphia humilis.* No endemic genera.

Niger (1,247,000 km²).—Two dubious endemic species (*Ipomoea ardissima, Vigna marchalii*).

Nigeria (877,000 km²).—It is instructive to consider this country under three regional headings:

(a) *Northern* (as defined in Hutchinson & Dalziel, 1954–1968) (662,263 km²). This is mainly in the Sudano-Zambezian Region (see Fig. 2). There are 39 endemic species (0.55%), examples of which are: *Dissotis graminicola, Habenaria nigerica, Huernia nigeriana, Indigofera latisepala, Protea argyrophaea, Pennisetum dalzielii, Psychotria dalzielii, Trochomeria dalzielii, Vernonia bauchiensis.* The lack of generic endemism, together with the prevalence of endemism

in widespread African genera, many extending to South Africa (e.g., *Protea*, *Huernia*), is noteworthy.

(b) *Western and Central* (see Table 5) (125,656 km^2). 38 endemic species (0.54%). Examples: *Begonia salisburyana*, *Brachystegia nigerica*, *Dissotis idanreënsis*, *Memecylon meiklei*, *Psammetes nigerica*. The low number of endemic species, notwithstanding the fact that this area is mainly in the Guineo-Congo Region, with rain forest well represented, is very significant, and is in strong contrast with (c) Eastern below. The genus *Psammetes* is endemic.

(c) *Eastern* (see Table 5) (76,364 km^2). 128 endemic species (1.81%). Examples: *Allexis obanensis*, *Ancistrocladus uncinatus*, *Butumia marginalis*, *Cola gigas*, *Crateranthus talbotii*, *Globulostylis talbotii*, *G. minor*, *Guaduella humilis*, *Hibiscus grewioides*, *Pohliella flabellata*, *Talbotiella eketensis*. The genera *Butumia*, *Crateranthus* and *Globulostylis* are endemic, and some of the species, e.g., *Cola gigas* and *Hibiscus grewioides* are outstandingly distinct. This evidence speaks for itself of the importance of eastern Nigeria as an area of high endemism, and of the remarkable contrast with the preceding regions of Nigeria. The area around Oban appears to be especially rich in endemics.

Cameroon (N.W.) (88,300 km^2).—Out of 156 endemic species (2.20%), about 45 appear to be confined to the Cameroon Mountain (some also extending to Bamenda). Examples of endemics are: Cameroon Mountain: *Afrardisia oligantha*, *Anthospermum cameroonense*, *Asparagus longipes*, *Begonia jussiaecarpa*, *Camptostylus ovalis*, *Deschampsia mildbraedii*, *Genyorchis macrantha*, *Helichrysum cameroonense*, *Hypseochloa cameroonensis*, *Mikaniopsis maitlandii*, *Peperomia vulcanica*, *Silene biafrae*, *Streptocarpus elongatus*, *Succisa trichotocephala*, *Uebelinia hispida*; other regions of Cameroon: *Bafutia tenuicaulis*, *Cylicomorpha solmsii*, *Inversodicraea keayii*, *Medusandra richardsiana*, *Oxyanthus setosus*, *Vincentella brenanii*. The genera *Hypseochloa* and *Bafutia* appear to be endemic.

The richness of eastern Nigeria is thus continued into Cameroon. It is remarkable that some of the outstanding rain forest endemics in each area have not been found in the other. Probably this does not just reflect undercollecting but is a real indication of narrow areas of distribution apparently not linked with any major topographical barriers.

The presence on the Cameroon Mountain of endemic species of genera of northern affinity is interesting, e.g., *Deschampsia*, *Silene*, *Succisa*, but probably reflects endemism in a more generalized African mountain flora rather than any special northern affinity particular to the Cameroon Mountain. The endemics on the mountain are found at all altitudes, from the rain forest on the lower slopes upwards, and this is reflected in the mixture of floristic elements represented in the examples given.

Fernando Po (Macías Nguema) (1,000 km^2).—49 endemic species (0.69%), a high figure considering the small area. Examples: *Cyathula fernandopoensis*, *Leptonychia* (4 species), *Melothria fernandensis*, *Psychotria crassicalyx*, *P. epiphytica*, *Sabicea urbaniana*, *Streptocarpus insularis*. Exell (1944: 51) quotes a figure of 99 endemic species for Fernando Po, but this was before the thorough revision undertaken for the second edition of the *Flora of West Tropical Africa*.

CENTRAL AND WEST-CENTRAL AFRICA

No single flora or enumeration has been written to cover all this area and therefore evidence has had to be assembled from a number of different works, mostly more or less incomplete, and these are cited under each country.

Chad (1,284,000 km^2).—I have not found any complete survey of the flora of Chad. Special studies have been made of the Saharan mountain ranges of Tibesti and Ennedi. Wickens (1976: 79) has examined the Tibesti specimens collected by Quézel and as a result estimates 38 endemic species from this range (7.2%). Gillet (1968) estimates 1% endemism for Ennedi. Elsewhere endemism is likely to be very low or none.

Central African Republic (493,000 km^2).—Sillans (1958: 197–203) estimated the total flora at about 3,600 species. Of these about 1,000 occur in the rain forest, with about 10 endemic (1%) and 2,600 in the savanna, with about 90 endemic (3.5%). The latter figure especially is probably too high. Examples of species endemics are: *Centaurea tisserantii*, *Combretum tisserantii*, *Monadenium chevalieri*, *Oryza tisserantii*. The two allegedly endemic genera, *Heimodendron* and *Tisserantodendron*, are neither now maintained.

Cameroon (475,000 km^2).—The *Flore du Cameroun* (Aubréville & Leroy, 1963–1975) is still very incomplete. Out of an estimated total of 6,500 flowering plants, 882 species have been described—about 15%. Of these, 110 (12.47%) are endemic. Multiplying this by a factor of 5.7, an approximate total figure of 627 endemics is obtained for the whole country. Generic endemism appears to be surprisingly low. In the estimated 15% of the flora dealt with, only one endemic genus, *Oriciopsis*, appears. *Eurypetalum* is almost endemic, being confined to the Cameroon and Equatorial Guinea. The country has great tracts of rain forest, and most of the endemic species are in the forest. Some examples are: *Balsamocitrus camerunensis*, *Aulotandra kamerunensis*, *Telfairia batesii*, *Dialium zenkeri*, *Talbotiella batesii*, *Brachystegia cynometroides*, *Pimpinella ledermannii*, *Strychnos mimfiensis*, *Octoknema dinklagei*, *Ocotea angustitepala*, *Scyphocephalium chrysothrix* and no less than 26 species of *Beilschmiedia*. The last-named is a most extraordinary concentration and deserves further study.

Equatorial Guinea (Rio Muni) (28,000 km^2).—Unfortunately this very interesting country has not received the critical botanical study that it merits. Guinea López (1946) gave a preliminary catalogue of the plants, but, as he admitted, it included many species that *might* occur but were not so far actually known to do so. Clearly, statistics of the known flora are not yet possible, but it is likely to be rich. One genus at least, *Chonopetalum* (Sapindaceae), is believed to be endemic. Of three new genera established by Guinea López (1946) only *Desmogymnosiphon* has not been sunk.

São Tomé (with Principe 964 km^2).—Of a total flora of 556 species (Exell, 1944) 108 are endemic (19.4%). *Heteradelphia paulowilhelmia* is a monotypic endemic genus. Endemic species include: *Begonia* (6 species), *Calvoa* (6 species), *Crossandra thomensis*, *Impatiens* (2 species), *Lobelia barnsii*, *Philippia thomensis*, *Pilea manniana*, *Podocarpus mannii*, *Rinorea* (3 species), *Staudtia pterocarpa*, *Thunbergianthus quintasii*.

Principe (with São Tomé 964 km²).—Out of 276 species 35 are endemic (12.7%) (Exell, 1944). *Principina grandis* is a monotypic endemic genus. Endemic species include: *Agelaea* (4 species), *Anthocleista stenantha*, *Casearia mannii*, *Chrysophyllum calophyllum*, *Dracaena monostachya*.

Annobon (17 km²).—Out of 115 species 17 are endemic (14.8%), (Exell, 1944). No endemic genera, but species include: *Agelaea annobonensis*, *Calvoa uropetala*, *Fagara annobonensis*, *Lachnopylis annobonensis*, *Rhynchelytrum reynaudioides*.

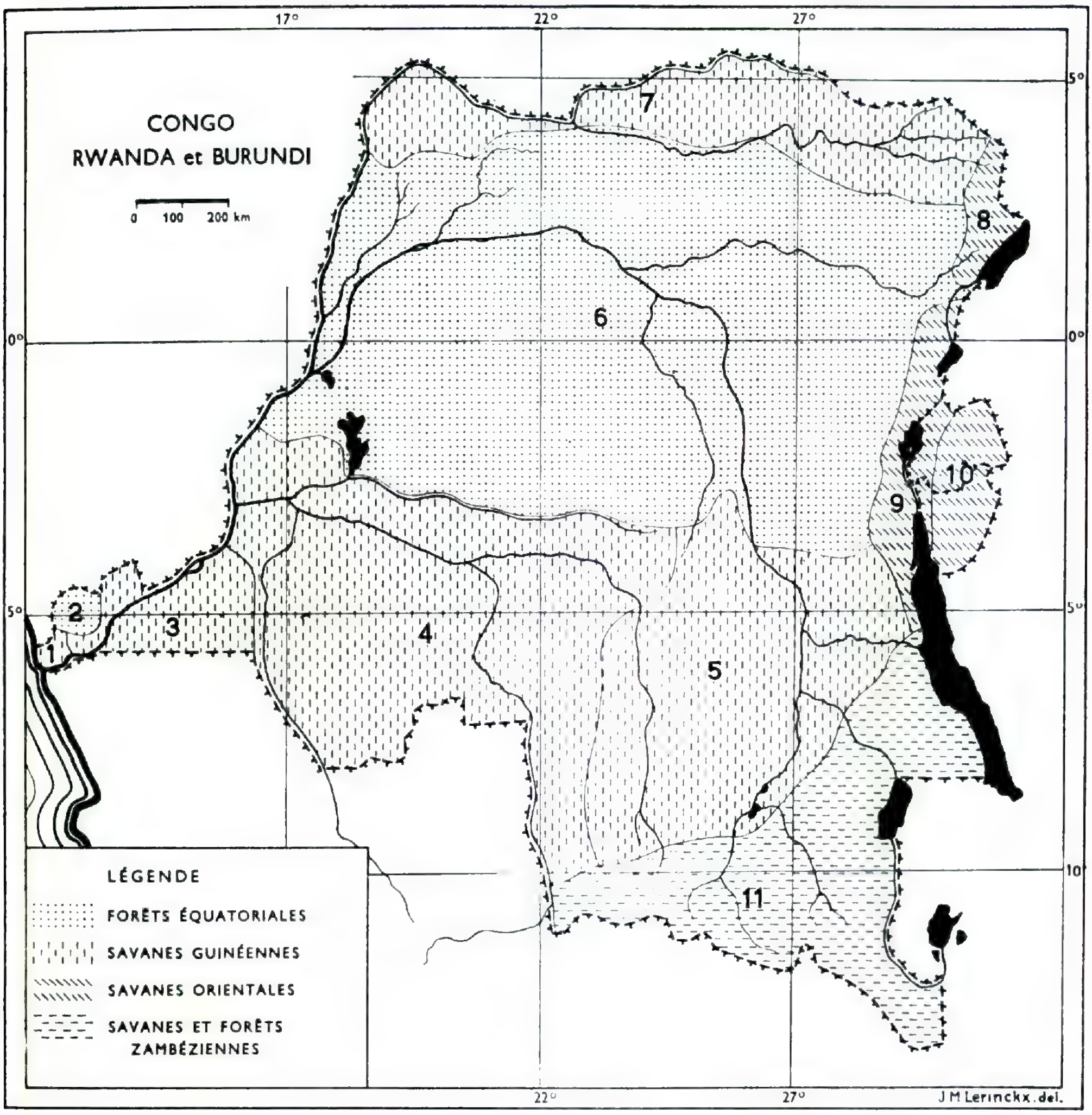
Gabon (267,000 km²).—The 23 parts of the *Flore du Gabon* so far published (Aubréville & Leroy, 1961–1972) (excluding the ferns) contain a total of 1,333 species, of which 243 are endemic (22.29%), a remarkably high figure. Unfortunately no estimate of the total flora is available, but Gabon is evidently, in terms of endemism, one of the richest countries in tropical Africa, although less so than Angola. In some groups, e.g., Leguminosae—Caesalpinioideae and Sapotaceae, the percentage endemism is much higher, 29.93% and 52.94% respectively.

In the parts so far published there are no less than 13 endemic genera: *Letestua*, *Lecomtedoxa* (5 species), *Tulestea* (3 species), *Iridosma*, *Temnopteryx*, *Neochevalierodendron*, *Sindoropsis*, *Augouardia*, *Paraberlinia*, *Pseudartabotrys*, *Coleactina*. The other endemic species include: *Cola* (8), *Dacryodes* (5), *Impatiens* (5), *Commelinidium gabunense*, *Costus* (6), *Beilschmiedia* (7), *Ocotea gabonensis*, *Gilbertiodendron* (8), *Monopetalanthus* (5), *Uvaria* (9), *Anonidium floribundum*, *A. le-testui*, *Polyceratocarpus pellegrinii*, and very many others, mostly in the forests.

Congo (Brazzaville) (342,000 km²).—Insufficient evidence for assessment. However, the country is likely to be comparable in endemism to the Gabon. The total number of species occurring has been estimated at about 4,000 (Bouquet, 1976).

Cabinda (7,770 km²).—Exell & Gonçalves (1973) analyzed a sample of 257 species and found 31 endemic (12.1%). This proportion is considerably lower than those for the Gabon and Angola and suggests that the richness of the rain forest flora may be decreasing southwards from the Gabon through Congo (Brazzaville) to Cabinda. Endemic species include: *Begonia mayombensis*, *Memecylon* (6 species), *Acioa dawei*, *Impatiens gossweileri*, *Crudia gossweileri*, *Chytranthus angustifolius*.

Zaïre (including Rwanda and Burundi) (2,345,000 km²).—This vast area has an estimated flora of about 10,000 species. Of these, 3,921 have been described in the first 10 volumes of the *Flore du Congo Belge et du Ruanda-Urundi* and the *Flore d'Afrique Centrale* (Robyns, 1965, supplemented by personal counting). A sample of about 39% is thus available. Of the total of 3,921, 1,280 are endemic to Zaïre (including Rwanda and Burundi), a remarkable proportion of 32.64%—apparently the highest proportion of endemism of any area in tropical Africa. Exell & Gonçalves (1973), working on a much smaller sample (1,218 species), estimated 38.2% for Zaïre. In this sample twelve endemic genera are included: *Hyalosepalum*, *Toussaintia*, *Afroguatteria*, *Gilbertiella*, *Thonnera*, *Ro-*



Territoires phytogéographiques par W. Robyns

1. Côtier. – 2. Mayumbe. – 3. Bas-Congo. – 4. Kasai. – 5. Bas-Katanga. 6. Forestier Central. – 7. Ubangi-Uele. – 8. Lac Albert. – 9. Lacs Édouard et Kivu. – 10. Ruanda-Urundi. – 11. Haut-Katanga.

Figure 5. Phytogeographical regions of Zaïre, Rwanda and Burundi as recognized by Robyns (1965). From *Flore du Congo, du Rwanda et du Burundi* Vol. 10 (1963).

bynsiophyton, Santaloidella, Pseudomacrolobium, Pynaertiodendron, Mildbraediodendron, Karina, Lebrunia. All or almost all are monotypic.

The endemism of Zaïre, Rwanda and Burundi repays closer analysis, as it is very far from being evenly distributed throughout the area. Robyns (1965) recognized 11 regions (Fig. 5) and I have tabulated the distribution of the 1,280 endemics on this basis in Table 11.

Of these areas, 2 and 6 are mainly rain forest, the others mainly savanna. Area 2 is small, 6 large. The high number of endemic species in area 6 is note-

TABLE 11. Zaïre, Rwanda and Burundi endemic species under the regions recognized by Robyns (1965).

Region	Number of Endemic Species	Region	Number of Endemic Species
1. Côtier	6	7. Ubangi-Uele	11
2. Mayumbe	4	8. Lac Albert	10
3. Bas-Congo	45	9. Lacs Édouard et Kivu	62
4. Kasai	80	10. Rwanda-Burundi	26
5. Bas-Katanga	36	11. Haut-Katanga	312
6. Forestier Central	233	12. In more than one of areas 1–11	275

worthy, but not unexpected, but the very high figure for Haut-Katanga is remarkable. This latter area, a mixture of forest and savanna in the Zambezian Domain is clearly a noteworthy center of endemism. There are for example, 69 endemic species of *Crotalaria* alone and 23 of *Cissus* (including *Cyphostemma*). It may well be that this area of high endemism is a continuation of the high endemism found in Angola. No such prolific generic speciation is to be met in area 6, Forestier Central. Here the highest numbers of endemic species under individual genera are *Salacia* (16), *Dichapetalum* (14), *Trichoscypha* (5). *Cola*, which one might expect to be well represented, has only one species endemic to area 6.

It is evident that Rwanda and Burundi have only a modest endemism. Lewalle (1975) discusses 8 endemic species in a mountain valley in Burundi near Lake Tanganyika.

NORTHEASTERN TROPICAL AFRICA

This area comprises the Sudan, Ethiopia, and Somalia. The island of Socotra, well known for its numerous and remarkable endemics, is not dealt with in the present paper. No single flora or checklist covers the entire region. There is a flora of the Sudan (Andrews, 1950–1956) and a checklist for the remainder (Cufodontis, 1953–1972). Unfortunately Andrews (1950–1956) does not give any data on general distribution, and Cufodontis (1953–1972), reflecting political changes during the course of the work, changed the boundaries of the areas under which species were recorded when more than halfway through the work. This results in the distribution data published after the change being often not directly comparable with those before, and also that very frequently it is not possible easily to assign species dealt with before the change to Ethiopia or Somalia as the boundaries then do not correspond with the boundaries now. It therefore seemed best to limit the present statistical survey to the sample of 2,638 accepted species published subsequent to the change, which are assignable to present-day political entities. The total flora of Cufodontis's region is estimated at 6,323 species (Cufodontis, 1953–1972: 1624).

Sudan (2,500,000 km^2).—Andrews (1950–1956) enumerated 3,137 species in all. For reasons given above, any exact estimate of endemism is not feasible. A cursory personal inspection of the flora leads me to estimate that the total number of species endemic to the Sudan is unlikely to exceed 50, which would be

1.6% of the above total. The work of Andrews is uncritical and incomplete and the percentage is likely to be reduced rather than increased. The Jebel Marra is an interesting and isolated mountain massif, but Wickens (1976) enumerated only 11 endemic species (1.2% of the total flora of Jebel Marra). Species endemic to Jebel Marra include: *Plectranthus jebel-marrae*, *Celsia sudanica*, *Kickxia dibolophylla* and *Gnaphalium marranum*. Other Sudan endemics include *Euphorbia consobrina*, *Jatropha gallabatensis*, *Combretum kabadensis*. However, a new critical flora, with a reassessment of the alleged endemics, would be well worthwhile.

Ethiopia (including Eritrea) (1,000,000 km^2).—Of the 2,638 species analyzed (see above), 553 were endemic to Ethiopia (20.96%). There is no doubt that Ethiopia, with its size and very diversified topography including great mountain ranges, has a rich endemic element in its flora. However, Cufodontis did not revise the flora critically and until this has been done, the proportions remain suspect and probably too high. There are a number of endemic genera including *Pseudozoysia*, *Simenia*, *Leptagrostis*, *Odontelytrum*, *Erythroselinum*, *Gymnosciadium*, *Lamellisepalum*, *Afrovivella*, *Sabaudiella*, etc.

Djibouti (*Territory of the Afars and Issars*) (23,000 km^2).—This small country, formerly French Somaliland, has apparently very few endemic species. Only one, *Kohautia gracillima*, was found among the 2,638 mentioned above.

Somalia Republic (700,000 km^2).—Of the 2,638 species analyzed (see above) 259 are apparently endemic (9.82%). However, the 2,638 species include a very large number not found in Somalia, so that the percentage is against a regional total comprising other countries and not of the Somalia flora as such, which is likely in total to be much smaller than that of Ethiopia. For this reason the true percentage of endemism is likely to be considerably higher, though against this must be set the fact that the Somali flora is as much in need of critical revision as that of Ethiopia, and there is no doubt that a significant proportion of the allegedly endemic species will not be maintained. Nevertheless the flora of the Somali Republic is a remarkable one with very many outstandingly distinct species found nowhere else. Significant proportions of the flora seem to be restricted to the Somali Republic but also occur in Harar Province of Ethiopia (21 out of 2,638: 0.8%), or Socotra (10 out of 2,638: 0.38%), or Arabia (38 out of 2,638: 1.44%). Furthermore, a very considerable number of species are restricted to the Somali Republic and northern Kenya, though I do not have exact figures for this.

Genera endemic to the Somali Republic include: *Lagenantha*, *Pleuropterantha*, *Pseudodigera*, *Neocentema*, *Puccionia*, *Cordeauxia*, *Dicraeopetalum*, *Scassellatia*, *Hypseloderma*, *Sennia*, *Rumicicarpus*, *Lithocaulon*, *Rhytidocaulon*, *Hyperaspis*, *Ghikaea*, *Chamaeacanthus*, *Lindauea*, *Golaea*, *Eionitis*, *Paolia*. This remarkable list, which will probably be lengthened, is a testimony to the interest and uniqueness of the flora of the Somali Republic.

EAST AFRICA: AREA OF FLORA OF TROPICAL EAST AFRICA

The published parts (to 1977) of the *Flora of Tropical East Africa* account for an estimated 40% of the total flora. However, this is already a sufficiently

TABLE 12. Endemism in East Africa: area of the *Flora of Tropical East Africa*. Total number of species: 4,412 ($\times 2.5 = 11{,}030$).

Region	Number	Percentage of 4,412
Endemic to 1 country	897	20.33
Endemic to 2 countries	199	4.51
Endemic to 3 countries	55	1.25
Endemic to more than 3 countries	10	0.23
Occurring more widely	3,253	73.73

large sample to give interesting evidence about the distribution of endemism in tropical east Africa without further adjustment. By multiplying by an appropriate factor (2.5) an approximation to totals can be obtained. In Table 12 percentages are given representing the relationship of the total endemism of each country to 4,412, the size of the regional sample.

The mention of "country" or "countries" in Table 12 means countries within the area of the *Flora of Tropical East Africa*. The high proportion of species endemic to one country contrasts with the much smaller figures for those species endemic to the area of the *Flora*, yet more widely spread than in one country. In other words, this emphasizes the prevalence of narrow species ranges in East Africa (cf. the proportion for West Africa in Table 10), and it is probably correlated with the much more diverse topography of East Africa, the frequency of isolated mountain ranges and peaks, and the fragmentation and isolation of forest areas.

A more detailed discussion of the endemism follows under each country.

Uganda (236,800 km²).—12 endemic species (0.27%) ($\times 2.5 = 30$). These are distributed among the provinces recognized in the *Flora of Tropical East Africa* as follows: U1, Northern: 3; U2, Western: 3; U3, Eastern: 1; U4, Buganda: 3. Two species occur in more than one province. Generic endemism is apparently nil or very small. The poverty in endemism of the Uganda flora is in very marked contrast to Kenya and Tanzania.

Kenya (582,600 km²).—106 endemic species (2.40%) ($\times 2.5 = 265$). The distribution according to the provinces recognized in the *Flora of Tropical East Africa* is as follows: K1, Northern Frontier: 22; K2, Turkana: 1; K3, Rift Valley: 3; K4, Central: 26; K5, Nyanza: 2; K6, Masai: 4; K7, Coast: 23.

In addition, 25 are endemic to Kenya but found in more than one province.

The above figures bring out the richness of K1, mainly because of the remarkable Somali element in the Kenya flora, especially in the northeast; the poverty of western Kenya (K2, 3, 5); the strong endemism of K4, in considerable measure due to the presence of Mount Kenya; and the richness of the coastal flora of K7. Generic endemism is low in Kenya but *Loewia* with two species and *Dibrachionostylus kaessneri* (K4) are to be mentioned.

The coastal flora in K7, although with a number of endemics, is really a northwards extension of a coastal element going far south into Tanzania and often extending on to Zanzibar. Of the 40% sample 77 species are endemic to K7 and also extend into the coastal areas of Tanzania and Zanzibar. Some gen-

era are endemic to this general area: *Angylocalyx*, *Asteranthe*, *Lettowianthus*, *Mkiluea*, *Ophrypetalum*. Lucas (1968) gives a useful list of species found in the Kenya coastal forests, including most of the endemics, which unfortunately are not distinguished as a separate category.

Tanzania (939,400 km²).—449 endemic species (10.18%) (× 2.5 = 1,122). The distribution according to the provinces recognized in the *Flora of Tropical East Africa* is as follows: T1, Lake: 13; T2, Northern: 20; T3, Tanga: 56; T4, Western: 24; T5, Central: 22; T6, Eastern: 77; T7, Southern Highlands: 70; T8, Southern: 56.

The figures show that Tanzania is outstandingly rich in endemics and that every province has a significant quota, though there seems a tendency for the numbers to be lower towards the northeast. T2 is noteworthy for the presence of Kilimanjaro, the highest peak in Africa; T3 contains the Usambara Mountains, with their sadly depleted but remarkably rich forests; T6 contains the Uluguru Mountains, as rich as the Usambaras, if not more so; T7 contains a rich endemic element in the high altitude grasslands of the mountain regions of southwestern Tanzania; and T8 contains a remarkable area towards the Mozambique frontier, very rich in endemism though apparently not isolated topographically and badly in need of further investigation in the field.

Polhill (1968) gave very useful lists of the known endemics from the Usambara Mountains (T3), the Uluguru and Nguru Mountains (T6), and the Lindi District (T8). It is therefore perhaps unnecessary to repeat here lists of endemic species, but mention should be made of generic endemism:

Usambaras: *Cephalosphaera usambarensis*, *Dolichometra leucantha*, *Englerodendron usambarense*, *Platypterocarpus tanganyikensis*.

Ulugurus: *Adenoplusia ulugurensis*, *Dionychastrum schliebenii*, *Pseudonesohedyotis bremekampii*, *Rhipidantha chlorantha*.

T8: *Farrago racemosa*, *Primularia pulchella*, *Vismianthus punctatus*.

Elsewhere in Tanzania: *Apochiton burttii*, *Peterodendron ovatum*, *Stuhlmannia moavi*.

This total of 15 genera, which will probably be increased, may be compared with 6 for Nigeria and 5 for Guinea.

Zanzibar (1,658 km²).—As one might expect from its size and proximity to Tanzania, there is little endemism. *Ipomoea zanzibarica* and *Aeschynomene zanzibarica* are said to be endemic in the sample of the East African flora analyzed (2 species, × 2.5 = 5) (0.05%).

SOUTHERN AND SOUTH-EAST TROPICAL AFRICA: AREAS OF FLORA ZAMBESIACA AND CONSPECTUS FLORAE ANGOLENSIS

The area numbered 10E is altogether within the area of the *Flora Zambesiaca* (Exell, Wild & others, 1960–1971), except for Angola. Unfortunately the floras are still far from complete. However, a sufficiently large proportion of each is in print to allow useful statistical deductions to be drawn.

Of *Flora Zambesiaca* the first two volumes are finished, together with part 1 of volume 3 and part 1 of volume 10. The pteridophyta, although published, have not been included here as the factors governing their distribution seem

TABLE 13. Statistics based on *Flora Zambesiaca*.

Approximate total of species in the whole flora (Exell, 1971)	6,000
Total of species, native and naturalized, in published sample surveyed	1,402
Percentage surveyed	23.37%
Species endemic to the area of the flora but not confined to one country	50 (3.57%)
Species endemic to single countries in the area of the flora	142 (10.13%)

often rather different from those of flowering plants, and their inclusion might well be a distorting factor in the rather limited samples dealt with here. Table 13 summarizes some of the main points.

It will be evident that the general percentages of endemism in the *Flora Zambesiaca* area are considerably lower than those for West Africa (10A) and East Africa (10D). As we shall see below, they are also considerably lower than for Angola. It is possibly worth noting that the total percentage endemism for the *Flora Zambesiaca* area is in close agreement with a figure of 13.2% quoted by Exell & Gonçalves (1973: 109) on a smaller sample.

The statistics drawn from the *Conspectus Florae Angolensis* will be considered under Angola among the accounts which follow of the individual countries in the area. Under each country the number of endemic species is given as revealed in the sample of 1,402 species surveyed, together with an estimate of the total arrived at by multiplying the number in the sample by a factor of 4.3, which represents the conversion of 1,402 to the estimated total of 6,000.

Mozambique (785,000 km^2).—51 endemic species (3.64% of sample); estimated total (51×4.3) of 219. Examples are: *Xylopia torrei*, *Bombax mossambicense*, *Glyphaea tomentosa*, *Impatiens suffulta*, *Dombeya leachii*, *Entada mossambicensis*, *Xylia mendoncae*. Generic endemism is low. Two monotypic genera occur: *Krauseola* and *Thespesiopsis*, of which the former may well be found also in northern Natal. Fryxell (1968) does not, however, consider the latter genus separable from *Thespesia*.

Mozambique has marginally more narrow endemics than any other country dealt with in *Flora Zambesiaca* (Zambia being next). Much of this comparative richness is probably due to a southerly extension of the high endemism noted above as a feature of the coast of Tanzania. The Usambara-Zululand Domain extends southwards from Tanzania along the coast to South Africa. However, in particular there is a region in northern Mozambique, extending to the Lindi District in Tanzania where there is a remarkable concentration of local endemism. The exact boundary of the area and the explanation of its existence still remain to be discovered. During the survey of the published parts of *Flora Zambesiaca*, at least 14 species were noted as restricted to northern Mozambique and southeastern Tanzania. These include such species as *Capparis orthacantha*, *Nectaropetalum carvalhi*, *Salacia orientalis*, *Pseudoprosopis euryphylla*, *Mimosa busseana*, *Acacia latistipulata*. This area is much in need of further study in the field.

Malawi (93,900 km^2).—16 endemic species (1.14% of sample); estimated total (16×4.3) of 69. Examples are: *Dasylepis burtt-davyi*, *Dovyalis spinosis-*

sima, Dombeya calantha, Impatiens quisqualis, Helichrysum whyteanum, Clutia brassii, Rhus monticola. The low level of general endemism is noteworthy and also the apparent total absence of endemic genera. Of the 16 species, six are apparently restricted to Mt. Mlanje. Wild (1964) lists 30 species endemic to Mlanje, and this has been commented on by Chapman & White (1970: 74) who note "the small number and critical nature" of the tree species represented and state that in the Afromontane tree flora "endemism is very weak and vicariism scarcely occurs." The affinity of the endemic element on Mt. Mlanje is in my view to be sought as much in South Africa as in tropical Africa. Similar opinions are voiced by Wild (1964) for the Chimanimani Mountains in Rhodesia.

Rhodesia (389,300 km^2).—22 endemic species (1.57% of sample); estimated total (22 × 4.3) of 95. Examples are: *Homalium chasei, Dianthus chimanimaniensis, Cyphostemma milleri, Bersama swynnertonii, Rhus wildii, Acacia chariessa.*

As for Malawi, the general level of endemism is low. The level of generic endemism is difficult to estimate, but probably very low, though including the outstandingly distinct *Triceratella* from the Limpopo River basin. Unfortunately only one gathering has been made (Brenan, 1961).

A considerable proportion of the total of endemic species in Rhodesia is likely to be confined to the Chimanimani Mountains. Wild (1964) lists 41 species endemic to this range, representing 4.6% of the total of 859 species occurring above 1,220 m (4,000 ft). Edaphic factors seem of especial importance in controlling the occurrence of endemism in Rhodesia. Wild (1964) notes that all or nearly all of the Chimanimani endemics are confined to areas of quartzite rock, and not found in the areas of shales and schists also well represented in this range. Wild (1965) listed 20 taxa, including at least 11 species endemic to the serpentines of the Great Dyke in Rhodesia. That serpentine rock often supports an unusual or unique flora is a well-known and widespread occurrence. Wild adduces evidence that high concentrations of nickel and chrome may be a leading factor. *Aristida hispidula* and *Rhus wildii*, for example, are endemics apparently linked with chrome.

Zambia (729,900 km^2).—49 endemic species (3.5% of sample); estimated total (49 × 4.3) of 211. Examples are: *Hypericum oligandrum, Monotes discolor, Dombeya brachystemma, Triumfetta* (3 species), *Biophytum richardsiae, Cissus fanshawei, Cyphostemma* (6 species), *Sorindeia rhodesica, Entada dolichorrhachis, Ozoroa* (4 species). Generic endemism appears to be low. The remarkable grass genus *Richardsiella* was described from the Abercorn area and the monotypic genus *Rastrophyllum* has been recently described (Wild & Pope, 1977) from Mwinilunga. The passifloraceous genus *Viridivia*, although not endemic to Zambia, appears only to occur elsewhere in southwestern Tanzania. The distribution of *Ageratinastrum* seems similar. The evidence is at present inadequate to comment clearly on the local distribution of endemism in Zambia, but out of the 49 endemics, 6 were restricted to the Solwezi-Mwinilunga area and 8 to the Abercorn area near Lake Tanganyika. It is possible, though unlikely, that this is partly due to both areas having been comparatively well collected.

Angola (1,246,700 km^2).—Exell & Gonçalves (1973) have carried out a very useful survey on the endemism of the flora of Angola, using as a basis volumes 2–4 of the *Conspectus Florae Angolensis* (Exell et al., 1937–1970), published during the period 1954–1970. The first volume was not used as being "now considerably out-of-date." The sample comprised 1,379 species. Fernandes (1971) estimated that the first four volumes of the *Conspectus Florae Angolensis* represented 40% of the total; roughly 10% of the total flora is thus dealt with in each volume, and Exell & Gonçalves's sample is thus roughly 30%.

Out of the 1,379 species, 378 (27.3%) were found to be endemic. This is a remarkable proportion—the more so in comparison with the other countries under 10E (3.64% for Mozambique and 3.5% for Zambia being the highest). The endemics were found to be most numerous in Huíla, Benguela, and Bié districts, respectively. It was considered that information was insufficient to list "district" endemics. Cabinda was, incidentally, not included in this exercise.

In the first four volumes of the *Conspectus*, eight genera are given apparently endemic to Angola (excluding Cabinda): *Mischogyne*, *Sedopsis*, *Caulocarpus*, *Carrissoa*, *Aizoanthemum*, *Spuriodaucus*, *Aframmi*, *Pseudoselinum*. Assuming on the basis given above that this is roughly 40% of the total, Angola appears to be one of the most important centers of endemism in southern tropical Africa.

COUNTRY ENDEMISM IN TROPICAL AFRICA

SUMMARY AND CONCLUSIONS

One of the objectives in the preceding pages has been to assemble the component parts in such a way that they might be put together into a more generalized coherent picture of the geographical distribution of endemism in tropical Africa.

The evidence set out in the last section of this paper is obviously very uneven. Sometimes it is based on a complete survey, but more often on more or less partial ones; sometimes the survey has been made for a single country, sometimes for a region. The deficiencies are only too manifest. Nevertheless it seemed worth while to make an attempt to bring the data together on a common basis.

Numbers of endemic species are important, but are inadequate alone. The Sudan with about 50 endemics is numerically richer than Principe with 35, but the concentration in the latter is far greater. Area is thus also important. Some combination of number and area seemed necessary. Evidence exists, as we have seen, either for exact figures or at least for approximate estimates of the total numbers of endemic species in most of the countries considered here. By dividing the number of endemic species (E) into the total area in square kilometers (A) of the country an Area-Endemism Index can be obtained varying from 0 to infinity.

The results are obviously unreliable in detail. In particular, probably no country has an even area spread of endemism—some areas in each country are richer than others. Yet the results are probably of the right order of magnitude and may serve to provide an objective though imperfect basis for assessing rela-

TABLE 14. Area-Endemism Index for tropical Africa. Figures followed by (e) represent an estimate based on a sample.

Country	No. of Endemic Species	A/E Index
Senegal	26	7,692
Guinea Bissau	0	–
Guinea Republic	88	2,840
Mali	11	136,363
Sierra Leone	74	977
Liberia	59	1,890
Ivory Coast	41	7,854
Ghana	43	5,541
Togo	20	2,800
Dahomey	11	10,236
Niger	2 ?	623,500
Nigeria		
N.	39	16,981
W. & C.	38	3,307
E.	128	596
Cameroon (N.W.)	156	566
Fernando Po (Macías Nguema)	49	2,041
Chad	50 (e)	25,680 (e)
Central African Republic	100 (e)	4,930 (e)
Cameroon	627 (e)	757 (e)
Equatorial Guinea	?	?
São Tomé Principe	143	7
Annobon	17	1
Gabon	1,115 (e)	239 (e)
Congo (Brazzaville)	?	?
Cabinda	310 (e)	251 (e)
Zaïre	3,200 (e)	733 (e)
Sudan	50	50,000
Ethiopia	1,105 (e)	905 (e)
Djibouti	2 (e)	11,500 (e)
Somali Republic	518 (e)	1,351 (e)
Uganda	30 (e)	1,893 (e)
Kenya	265 (e)	2,198 (e)
Tanzania	1,122 (e)	837 (e)
Zanzibar	5 (e)	327 (e)
Mozambique	219 (e)	3,584 (e)
Malawi	69 (e)	1,360 (e)
Rhodesia	95 (e)	4,097 (e)
Botswana	17 (e)	33,823 (e)
Zambia	211 (e)	3,459 (e)
Angola	1,260 (e)	989 (e)

tive endemism. In Table 14 the results are set out. The figures for endemism when followed by "(e)" represent an estimate based on a sample.

The basis of certain of the above figures in the left-hand column needs stating. For Ethiopia it is assumed that 553 endemics (see p. 467) represents a sample of about half the total, and the same applies to Somalia (see p. 467 when the figure 259 is multiplied by 2 for the above table).

The distribution of endemism in Nigeria is so uneven (see p. 461–462) that an overall figure would be misleading and the A/E Index is therefore given for the three regions individually recognized.

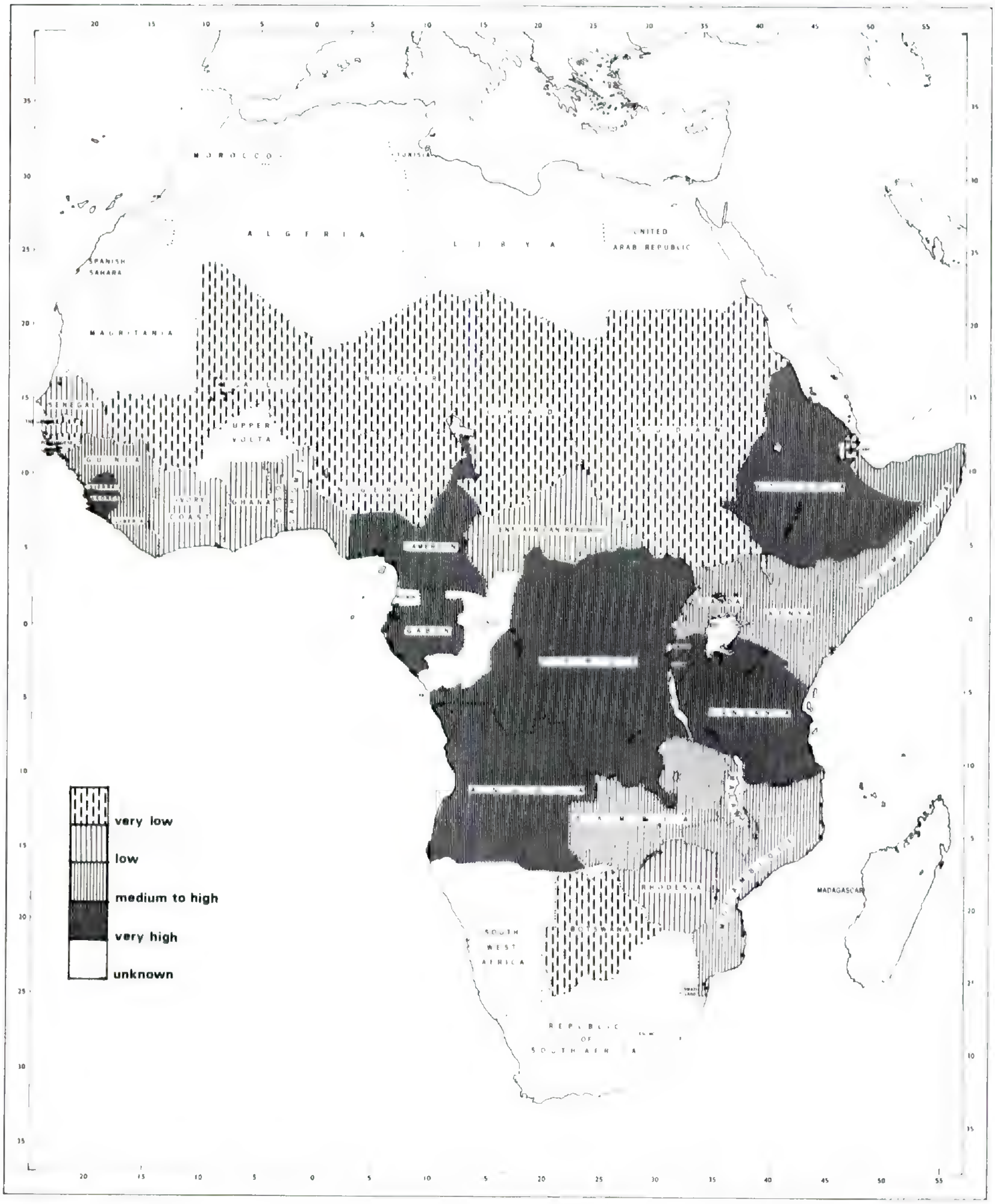


FIGURE 6. Categories of endemism in tropical Africa assessed by countries based on Table 12. Although Zaïre (Congo on map) on this basis is a country of high endemism, the high overall assessment reflects two separate areas especially rich: Bas-Katanga joining Angola and Tanzania; and Forestier Central adjoining Congo-Brazzaville which is probably rich in endemism as is the adjacent Gabon.

The above figures enable a rough categorization to be made:

(a)	Very Low	:	10,000 or more
(b)	Low	:	4,000–10,000
(c)	Medium–High	:	1,000–4,000
(d)	Very High	:	0–1,000

The distribution of the categories within tropical Africa is given on the accompanying map (Fig. 6).

It is hoped that the various incomplete regional floras or lists for tropical Africa may be finished as soon as possible so that a clearer and more exact picture may be obtained of this aspect of its flora. On the basis its future management and preservation may be undertaken on a basis of better evidence than has hitherto been available.

With the speed of destruction or modification of tropical vegetation types under the pressures of increasing population and modern technology, the need for urgent conservation measures is increasingly pressing, but the evidence upon which to establish priorities has been often imperfect or lacking. Obviously the degree of endemism (or uniqueness) in any given area is a most important factor. Where endemism is low the danger of irreparable loss is lessened, and *vice versa*. The best and most economical way of conserving threatened species is to conserve the habitat. In the past the establishment of reserves or national parks has often been made with insufficient account taken of the uniqueness of what is preserved and deserving areas have been neglected. A knowledge of local endemism will help to make a better basis for future policy.

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ANALYSIS OF THE FLORA OF MEDITERRANEAN AND SAHARAN AFRICA[1]

P. Quézel[2]

Abstract

After defining the state of knowledge and reviewing national inventories, the author looks at the reasons which led him to study Mediterranean and Saharan Africa and to detail their biogeographical significance.

For Mediterranean and Saharan Africa, the generic and specific richness, the richness of endemics, and the entire biogeographical range are first analyzed at the family level. In the second part, the various biogeographical elements which play a part in the formation of the floras at the generic and specific levels are defined; several examples are provided respectively for the Mesogean (Mediterranean, Saharo-Arabian and Irano-Turanian) and tropical elements. A third part is devoted to endemism: first generic and specific endemism, then the biogeographical significance of the endemic taxa. It appears that the flora of Mediterranean Africa is about three times richer than that of Saharan Africa and that endemism there is two times greater. Whereas the flora of Mediterranean Africa is for the most part made up of Mediterranean taxa, in Saharan Africa there is a nearly equal distribution of Mediterranean, Saharo-Arabian, and tropical elements. These characteristics are related to the hostile ecological conditions which govern the Sahara now, but also reflect the climatic disturbances which took place during the Pleistocene. A special chapter is devoted to a discussion of the historical interpretation of the flora of Mediterranean and Saharan Africa, taking into account the new data provided by paleoclimatology and paleobotany. It is concluded that the Mediterranean flora is relatively old and goes back at least as far as the middle Miocene, whereas the present Saharan flora is a reflection of intense climatic changes which have severely affected this region since the Pliocene. In each of these cases emphasis has been placed on the role elements of African origin played in the development of the present flora.

I—Introduction

A little more than the northern quarter of the African continent escapes tropical floristic influences. This rather heterogeneous unit poses many problems of biogeographical and historical interpretation, but is nevertheless rather well known from the point of view of floristic composition.

The territory covered by this study includes the whole of Mediterranean Africa, but also the Sahara down to its southern limits, some close approximations of which will be defined below.

It seemed more meaningful and realistic to abandon the artificial framework of political boundaries for the infinitely more realistic one of biogeographical units.

I. 1—the level of knowledge

In the Maghreb the present state of floristic knowledge of vascular plants, which alone are discussed in this work, can be considered satisfactory such as was stated in the recent symposium of the Centre National de la Recherche Scientifique devoted to the flora of the Mediterranean basin held in Montpellier,

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Ann. Missouri Bot. Gard. 65: 479–534. 1978.

0026-6493/78/0479–0534/$05.75/0

1974. Without going into detail, it should be remembered that the state of our knowledge is being published in the *Flore de l'Afrique du Nord* by R. Maire (1952–1976), and that 14 volumes of it have already appeared. Various catalogs and regional floras also reflect floristic knowledge relating to the countries of the Maghreb. For example Jahandiez & Maire (1931–1934), Emberger & Maire (1941), Sauvage & Vindt (1952, 1954) for Morocco, Quézel & Santa (1962–1963) for Algeria, Cuénod (1954) for Tunisia, and Ozenda (1958) for western and central Sahara.

In Libya and in Egypt valuable data are also available (Boulos, 1975) from several publications, in particular for Libya those of Durand & Baratte (1910) and of Pampanini (1931), and for Egypt those of Täckholm (1956, 1974).

On the other hand, for the countries situated further south in the Saharan region, data are much sparser, and one is often obligated to consult partial inventories. The list of these (Quézel, 1965) has not undergone significant modification since Quézel (1965), with the exception of the work by Scholz (1966, 1974) and Scholz & Gabriel (1973).

I. 2—NATIONAL INVENTORIES

This approach, although not very significant, deserves nevertheless to be considered because it furnishes a preliminary idea of the floristic richness of Northern Africa.

For the countries of the Maghreb, Sauvage (1975) estimates that Morocco has approximately 3,700 species distributed among 920 genera and 124 families. For Algeria and Tunisia (Quézel & Bounaga, 1975), there are about 3,300 species (about 3,100 for Algeria and 2,100 for Tunisia, Le Houérou, 1975) 980 genera and 130 families. As for Libya (Boulos, 1975), it has approximately 1,600 species and Egypt somewhat more than 2,000 (including Sinai).[2]

In contrast, it is difficult to state exactly the floristic richness of the countries of the Sahel, a part of which territory is to be considered here. Saharan Mauritania and the former Spanish Sahara have a flora which can reasonably be estimated (Guinea, 1949; Monod, 1938, 1939, 1952; Murat, 1944; Sauvage, 1946, 1949; Naegele, 1958) at about 600 species. The figures are even smaller for Saharan Mali and Niger (probably less than 250 species). Northern Chad, however, due to the relative richness of Tibesti (Maire & Monod, 1950; Quézel, 1958) has at least 550 species. Saharan Sudan was not included in this work, but besides the mountains adjacent to the Red Sea, which represent a very special case, the real Saharan zone of this country probably has no more than 200 species.

I. 3—THE LIMITS OF THE ZONE STUDIED

Even though nearly all biogeographers who have worked in northern Africa agree on a general interpretation of the major limits (Monod, 1957; Quézel, 1965; Barry et al., 1976), a certain number of problems deserve, nevertheless, to be stated and discussed. One point that is particularly important is to trace

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[2] The Sinai Peninsula, being situated geographically in Asia, will not be considered here.

the limits between the Holarctic Floristic Kingdom and the Paleotropical Floristic Kingdom.

It should be remembered that the Holarctic Kingdom in northern Africa is represented by two floristic regions: the Mediterranean Region and the Saharo-Sindian, or better, Saharo-Arabian (sensu Zohary, 1973) Region. The existence of vestiges or Irano-Turanian relicts, discussed especially by Zohary (1962), seems difficult to accept for bioclimatic, floristic, or dynamic reasons. Actually, these regions have numerous common characteristics, and biogeographers are more and more tempted to put them under one subkingdom which may most appropriately be called the "Mesogean." This viewpoint, already suggested by Gaussen (1954) and accepted from the standpoint of bioclimates by Emberger (1945), Daget (1977), and Nahal (in particular 1976), underlies the narrow genetic and historical affinities that exist in the entire domain of the old Tertiary Mesogean (Tethys).

Be that as it may, and without going into discussions which go well beyond the limits of this study, and without establishing limits too strictly, it is possible and practical to accept the isohyet of 100 mm (Capot-Rey, 1953; Quézel, 1965) to limit the southern extension of the Mediterranean Region.

It is evident that this arbitrary boundary corresponds well to ecological and biogeographical realities, in spite of many exceptions, and also in spite of the opinion of Emberger (1945) and, more recently, Barry et al. (1976) who tend to move the boundary of the Mediterranean Region to the south, essentially for bioclimatic reasons for the first author (annual rainfall pattern still of a Mediterranean type) or genetic reasons for the second authors (flora still rich in Mediterranean elements). I would prefer to call it "Mesogean."

One must recognize, however, that the problem of the boundaries between the Saharo-Arabian Region and the Sudano-Angolan Region, and in fact between the Holarctic and Paleotropical Kingdoms (Monod, 1957) is much more difficult to resolve. Indeed, as I have shown (Quézel, 1965), whereas a large portion of the Sahara belongs, for the most part, to the Saharo-Arabian Region, toward the south the question becomes complicated by the extension, or even predominance, of the elements of tropical origin (without forgetting residual Mediterranean taxa, particularly on high Saharan mountains). These characteristics are basically connected to the large climatic fluctuations that took place in the Sahara during the entire Quaternary, and of which the latest changes are quite close to us, probably less than 5,000 years (Pons & Quézel, 1956, 1957; Quézel & Martinez, 1961), and brought with them vast floristic mixing. The effects of these changes are still being felt. Its interpretation could scarcely be established at anything other than the level of a precise analysis of present ecological factors. These difficulties led us to define as "regional complexes"[3] areas where Saharan, tropical, or even Mediterranean floristic elements coexist in more or less equal numbers.

It is certainly appropriate to keep the flora of the zonal complexes, "Mediter-

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[3] One hears today the term "zonal complexes," a term whose biogeographical value is less precise.

TABLE 1. Phytogeographical subdivisions of the flora of North Africa.

	HOLARCTIC KINGDOM					PALEOTROPICAL KINGDOM	
	Mesogean Subkingdom					African Subkingdom	
	Mediterranean Region		Saharo-Arabian Region	Complex Zones		Soudano-Angolan Region	
	West-Mediterranean Subregion	East-Mediterranean Subregion	Saharan Subregion	Mediterranean-Saharo-Sudanian Complex Zone	Saharo-Sudanian Complex Zone	Saharo-African Subregion	Sahelian Subregion
DOMAINS	Mediterranean North-African (1) Steppic North-African (2)	Cyrenian North-African (3) Steppic Eastern-African (4)	N.W. Saharan (5) N. Saharan (6) Oceanic Saharan (7) N.E. Saharan (8)	Saharan High Mountains (9)	Central Saharan (10) Eastern Saharan (11) Western Saharan (12)	Southern Saharan (13)	Northern Sahelian (14)

ranean-Saharo-Arabian-Sudano-Angolan" (high Saharan mountains) and Saharo-Arabian-Sudano-Angolan (western, central and eastern Sahara) in the framework of this study. However, the case of the southern Saharan fringe (southern Sahara) can be disputed. That zone is characterized by a very poor flora, it is true, but one of essentially African origin which permits its integration into a particular subregion (Saharo-African Subregion). This subregion is included in our study since in physiognomy it much resembles a Saharan country, because its exact boundaries to the north are extremely difficult to state exactly, and because on the floristic level, it actually only has a very small number of species, probably less than 50.

The southern boundary established in this study (with the exceptions noted above) is therefore the physiognomically southern boundary of the Sahara, a boundary which is made real by the appearance of an ephemeral, but nearly continuous plant cover which corresponds noticeably to the 150 mm isohyet (Capot-Rey, 1953; Quézel, 1965).

These biogeographic interpretations have been schematically indicated in Table 1 and Fig. 1.

I. 4—SOME PROBLEMS RELATING TO FLORISTIC ANALYSIS

If the floristic inventory of northern Africa can be considered, as we have seen, practically completed, certain problems, nevertheless deserve attention.

Indeed, at the outset, from the point of view of nomenclature the study of the flora of North Africa or of the Sahara has not followed that of the European flora, for example, and one has generally stayed with Maire's concepts which, in many cases, are in need of revision. Since this work is currently in progress, it has been difficult to consider it here, except in some classical cases. Nor is that our purpose here.

As in all attempts at synthesis, the results obtained can vary with different conditions, especially according to the species concept. Our point of view is perhaps too narrow, but we have hesitated to accept a certain number of still debatable positions concerning certain critical genera. The case of the genus *Rupicapnos* is probably the most obvious. Pugsley (1917) recognized some 30 species of it in North Africa, nearly one per locality. The arguments and the criticisms of this author remain debatable, in particular if one studies the question at the population level and not by herbarium specimens, and following Maire (1952–1976) only three species are kept in this genus.

Certain critical genera are also very poorly known, in particular in the Maghreb. For example, it is evident that the 10 species kept in the genus *Rubus*, the 12 in *Rosa*, or the dozen in *Hieracium* or *Crepis* are, from all evidence, very much below what is actually there.

Likewise, a precise taxonomic analysis will certainly lead to a revision of our position on the value of a certain number of genera and species, whether they might be synonymized specifically with certain taxa of the Near East, or whether entities currently considered homogeneous might be separated.

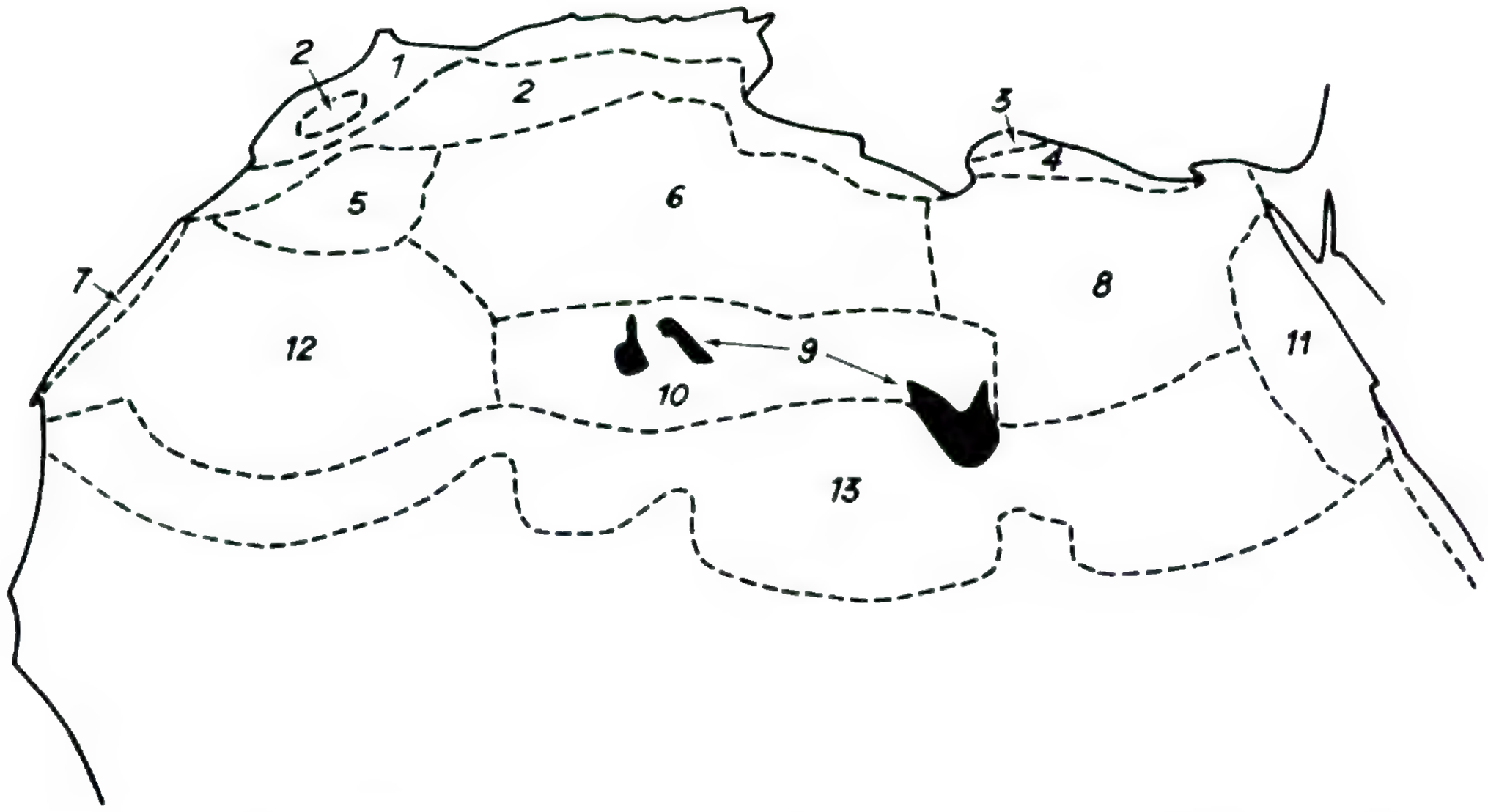

FIGURE 1. Phytogeographical subdivisions of Mediterranean Africa and Saharan Africa. —1. Mediterranean-Northern African Domain.—2. Steppic-Northern African Domain.—3. Cyrenian-Mediterranean Domain.—4. Steppic-Eastern African Domain.—5. Northwestern-Saharan Domain.—6. Northern Saharan Domain.—7. Oceanic Saharan Domain.—8. Northeastern Saharan Domain.—9. Saharan-High Mountain Domain.—10. Central Saharan Domain. —11. Eastern Saharan Domain.—12. Western Saharan Domain.—13. Southern Saharan Domain.—14. Northern Sahelian Domain.

In view of this, the figures provided below can only be considered to be estimates. They are, however, significant because, despite these reservations, the fact remains that the Mediterranean African and Saharan floras are the best known and most studied on the African continent.

Therefore we shall study below and successively the floras of Mediterranean and Saharan Africa. This plan will obviously lead to the appearance of a certain number of species in the two chapters; in fact, this number is not very high and does not exceed 200. Likewise, some tropical species present in the southern Sahara especially will reappear in the statistics for tropical Africa. Here again the number of these species is not very large and probably even less than the number referred to above.

Finally let us note that a certain number of difficulties appeared during the establishment of the biogeographical spectrum. It is basically the problem presented by "connecting" (Eig, 1931) species of two or more regions. Without extending their interpretation too far, they have generally been partially counted at the level of biogeographical groups (0.5 and 0.5, for example, for a connecting Saharan-tropical species). We have, however, avoided showing decimals in the summary tables, decimals which would have given an unwarranted impression of precision. Also we have not taken into account the species obviously adventive or introduced by man, and whose naturalization cannot be established.

II.—MEDITERRANEAN AFRICA

Mediterranean Africa includes mainly the three countries of the Maghreb to

the north of the southern edge of the Bani and the Saharan Atlas, as well as the Libyan coastline (including the Djebel Nefoussa in Tripolitaine and Akhbar in Cyrenaïque), and the Egyptian coastline, covering an area on the order of 900,000 km^2.

The countries of the Maghreb, which represent about 800,000 km^2 of the total, constitute far and away the most remarkable unit, the richest from the floristic point of view, and one in which historical and geomorphological factors have allowed the development of the greatest number of endemics. The eastern unit (Libya and Egypt) is infinitely poorer and less diversified, but still presents several problems which will be examined later on.

II. 1—THE FAMILIES

II.1.1—*Generic and Specific Richness* (Table 3)

In Mediterranean Africa, 130 families of phanerogams and 18 families of vascular cryptogams are represented.

Their generic representation is quite variable, and only 2 families have more than 100 genera (Gramineae 114, Compositae 106), 2 have more than 50 (Cruciferae 84, Umbelliferae 61), 5 more than 20 (Leguminosae 49, Labiatae 34, Caryophyllaceae 32, Boraginaceae 26, Liliaceae 24), and 6 more than 10 (Chenopodiaceae 19, Rosaceae 19, Scrophulariaceae 18, Orchidaceae 13, Ranunculaceae 13, Papaveraceae 11); the Filicales contain 15 genera. Fourteen families have from 6 to 10 genera, 52 have 2 to 5, and 55 have only one.

From the standpoint of richness of species only 8 families exceed 100 species: Compositae 563, Leguminosae 432, Gramineae 338, Caryophyllaceae 227, Labiatae 222, Cruciferae 215, Scrophulariaceae 145, and Liliaceae 113. Ten families have between 99 and 50 species: Boraginaceae 86, Cyperaceae 80, Ranunculaceae 64, Euphorbiaceae 62, Cistaceae and Rosaceae 60, Chenopodiaceae 58, Orchidaceae 54, Papaveraceae 52, and Rubiaceae 50. Fifteen families have 49 to 20 species: Geraniaceae 47, Plumbaginaceae 46, Crassulaceae 43, Orobanchaceae 40, Campanulaceae 37, Polygonaceae 36, Iridaceae and Malvaceae 32, Convolvulaceae 31, Juncaceae 29, Valerianaceae 26, Resedaceae 25, Dipsacaceae 24, Plantaginaceae 23, and Amaryllidaceae 20. Altogether the Filicales contain 37 species. Fifteen families possess 19 to 10 species: Linaceae, Saxifragaceae and Solanaceae 18, Thymelaeaceae 17, Gentianaceae and Primulaceae 16, Onagraceae 14, Potamogetonaceae 12, Aizoaceae, Amaranthaceae, Asclepiadaceae and Caprifoliaceae 11, Salicaceae, Violaceae and Zygophyllaceae 10.

Without carrying this analysis further, it is appropriate to point out that 10 families are represented by 4 species, 11 by 3, 18 by 2 and 28 are monospecific in Mediterranean Africa.

II.1.2—*Biogeographical Significance at the Family Level*

Without entering further into an exact analysis, and without considering the biogeographical value of the endemics, it is nevertheless worthwhile to point

out that in Mediterranean Africa, the great majority of families is essentially made up of species linked to the Mediterranean element. However, several exceptions should be noted.

Thus the major element is no longer Mediterranean but "northern" in the following families of several species: Aceraceae, Alismataceae, Betulaceae, Callitrichaceae, Ceratophyllaceae, Cyperaceae, Elatinaceae, Grossulariaceae, Haloragidaceae, Hydrocharitaceae, Juncaceae, Juncaginaceae, Lemnaceae, Lentibulariaceae, Loranthaceae, Nymphaeaceae, Onagraceae, Orchidaceae, Primulaceae, Ranunculaceae, Rosaceae, Salicaceae, and Sambucaceae. The same is true for the following monospecific families: Adoxaceae, Aquifoliaceae, Araliaceae, Butomaceae, Dioscoreaceae, Illecebraceae, Juglandaceae, Menyanthaceae, Monotropaceae, Najadaceae, Parnassiaceae, Sparganiaceae, and Taxaceae. The majority of these families is essentially composed of aquatic or largely hygrophilous taxa which escape climatic influences, or have only a small number of species, which creates a deceptive statistical interpretation. The Rosaceae, Ranunculaceae, Orchidaceae, and Primulaceae deserve mention; these relatively important families are in fact the only families in Mediterranean Africa that have a predominance of elements of northern stock.

Also mentioned should be families in which the majority of the species are related to cosmopolitan or more or less ubiquitous lines: Aizoaceae, Amaranthaceae, Hydrocharitaceae (already cited above), Najadaceae, Nyctaginaceae, Onagraceae, Oxalidaceae, Polygonaceae, Portulacaceae, Potamogetonaceae, Typhaceae, Trappaceae, Verbenaceae, and Zosteraceae. Here again mainly aquatic or even clearly anthropophilous (?) families predominate; the Aizoaceae and the Nyctaginaceae have, however, tropical affinities.

II.1.3—*Endemic Richness at the Family Level*

Endemic richness is quite variable. If limited to a strict inventory, the figures are the following: more than 100 endemic species: Compositae 231, Leguminosae 105; more than 50 endemic species: Labiatae 99, Caryophyllaceae 75, Cruciferae 72, Umbelliferae 53, Scrophulariaceae 50; more than 20: Gramineae 42, Liliaceae 25, Boraginaceae 23; more than 10: Geraniaceae and Plumbaginaceae 17, Campanulaceae 16, Crassulaceae and Euphorbiaceae 13, Cistaceae, Papaveraceae and Resedaceae 11, Ranunculaceae 10; more than 5: Iridaceae and Orobanchaceae 9, Chenopodiaceae, Convolvulaceae and Rubiaceae 8, Dipsacaceae, Linaceae and Saxifragaceae 7, Malvaceae and Rosaceae 6, Orchidaceae and Polygonaceae 5; with 4 endemic species: Amaryllidaceae, Plantaginaceae, Thymelaeaceae, Valerianaceae and Violaceae; with 3 endemic species: Gentianaceae, Onagraceae, Polygalaceae, and Zygophyllaceae; with 2 endemic species: Aizoaceae, Asclepiadaceae, Hypericaceae, Primulaceae, Santalaceae, and Selaginaceae. Finally the following families are represented by only one endemic species: Anacardiaceae, Araceae, Berberidaceae, Capparaceae, Caprifoliaceae, Commelinaceae, Fagaceae, Frankeniaceae, Juncaceae, Najadaceae, Pinaceae, Rutaceae, Sapotaceae, and Solanaceae.

Sixty-nine families have no endemic species in Mediterranean Africa. Among

TABLE 2. Distribution of the total number of species in Mediterranean Africa into its biogeographical subdivisions.

Subdivision	Number	Percentage (%)
Total genera	916	
Total species	4034	
Endemics	1038	25.7
North African	78	1.9
Ibero-Mauritanian	408	10.1
Macaronesian	27	0.5
Western Mediterranean	321	7.9
Eastern Mediterranean	160	3.9
Mediterranean	873	21.6
Irano-Turanian	33	0.8
Saharo-Sindian	122	3.0
Atlantic	63	1.5
European and Eurasian	528	13.1
Paleotemperate	73	1.8
Circumboreal	40	0.9
Tropical	56	1.3
Cosmopolitan or other distribution	214	5.3

these, only 5 are represented by more than 10 species. They are the following: Cyperaceae 80, Potamogetonaceae 12, Amaranthaceae 11, and Salicaceae and Tamaricaceae 10.

II.1.4—*The Global Biogeographical Spectrum*

For the entire flora of Mediterranean Africa, maintaining the accepted biogeographical subdivisions, the percentages are given in Table 2.

II.2—THE PRINCIPAL BIOGEOGRAPHICAL ELEMENTS

We shall look at them successively, ending with a study of the endemics.

II.2.1—*Mediterranean Taxa*

II.2.1.1—*Ibero-Mauritanian Taxa.*—Ibero-Mauritanian taxa represent about 10% of the Mediterranean African flora, and naturally are found principally in the Maghreb. Regrouped under this heading are the following (Quézel, 1957) elements: Ibero-Mauritanian, in the strict sense, Betico-Atlas and Pyrenees-Atlas. Differentiation of these three groups is not always easy, but schematically they certainly correspond to different groups.

The Ibero-Mauritanian group is present in more than half of the families; however, it plays a particularly important role in the following families, where it represents percentages greater than 10:[4] Liliaceae: *Braxireon**; Amaryllidaceae: *Leucojum*, *Lapiedra**, *Narcissus*; Boraginaceae: *Echium*; Campanulaceae: *Campanula*, *Jasione*; Caryophyllaceae: *Arenaria*, *Minuartia*, *Silene*; Cistaceae: *Cistus*, *Helianthemum*, *Halimium*; Compositae: *Senecio*, *Centaurea*, *Andryala*, *Carduus*,

[4] The Ibero-Mauritanian genera are followed by an asterisk.

*Prolongoa**, *Otospermum**, *Daveaua**, *Glossopappus**; Crassulaceae: *Sedum*; Cruciferae: *Diplotaxis*, *Alyssum*, *Matthiola*; Ericaceae; Euphorbiaceae: *Euphorbia*; Gramineae; Iridaceae: *Iris*, *Romulea*, Labiatae: *Teucrium*, *Thymus*; Leguminosae: *Retama*, *Stauracanthus*, *Erinacea**, *Ulex*, *Cytisus*, *Genista*, *Ononis*, *Anthyllis*; Malvaceae; Orobanchaceae; Plumbaginaceae; Rosaceae; Rubiaceae; Saxifragaceae; Solanaceae: *Triguera**; Saxifragaceae; Scrophulariaceae: *Linaria*, *Odontites*; Thymelaeaceae; Umbelliferae: *Eryngium*, *Ammiopsis**, *Brachyapium*, *Bupleurum*; Valerianaceae; Papaveraceae: *Sarcocapnos**, *Rupicapnos**, *Platycapnos*, *Ceratocapnos*.

Here are some particularly significant examples at the species level:

Betico-Rifaines species: *Abies pinsapo*, *Drosophyllum lusitanicum*, *Eryngium glaciale*.

Betico-Atlas species: *Anthyllis warnieri*, *Arenaria pungens*, *Andryala aghardii*, *Sedum melanantherum*, *Pseudocytisus integrifolius*, *Poterium ancistroides*.

Pyrenees-Atlas species: *Potentilla alchimilloides*, *Matthiola perennis*, *Valeriana globulariaefolia*, *Saxifraga longifolia*, *Lonicera pyrenaica*.

II.2.1.2—*Macaronesian Taxa*.—In Mediterranean Africa, Macaronesian taxa are mainly found on the Atlantic coast of Morocco, especially in the Sous valley. They represent (without counting the endemics of Macaronesian stock) less than 30 species. Especially important are the following: *Davallia canariensis*, *Asparagus pastorianus*, *Traganum moquini*, *Chenolea tomentosa*, *Euphorbia balsamifera*, *E. obtusifolia*, *Helianthemum canariense*, *Polycarpaea nivaea*, *Drusa oppositifolia*, *Astydamia latifolia*, *Zygophyllum fontanesii*, *Hypericum coadunatum*, *Rhus albida*, *Lithospermum microspermum*, *Carraluma buchardii*, *Phagnalon calycinum*, *Asteriscus odorus*, *Andryala canariensis*, and *Sonchus pinnatifidus*.

II.2.1.3—*Western Mediterranean Taxa*.—Slightly less numerous than the Ibero-Mauritanian (321), the Western Mediterranean taxa still represent approximately 8% of the entire flora. Actually, also included here are a certain number of Centro-Mediterranean or even Tyrrhenian elements, which are not very abundant and from which it is appropriate to cite in particular: *Silene sedoides*, *Rosa serafini*, *Vicia barbazitae*, *Sideritis romana*, *Stachys marrubiifolia*, and also the genus *Tetragonolobus*.

The Western Mediterranean taxa are especially frequent in the following families: Boraginaceae 6, Caryophyllaceae 20, Cistaceae 11, Compositae 52, Cruciferae 12, Euphorbiaceae 9, Gramineae 21, Labiatae 19, Leguminosae 43, Liliaceae 15, Scrophulariaceae 11, and Umbelliferae 12.

Among the genera especially representative of this biogeographical subdivision are: *Chamaerops*, *Ampelodesmos*, *Avellinia*, *Wangenheimia*, *Aphyllanthes*, *Ionopsidium*, *Succowia*, *Solenanthus*.

II.2.1.4—*Northern Mediterranean Orophilous Taxa*.—Some species, in general largely present on the mountains of the northern Mediterranean slope from which they spread northward, strangely appear in North Africa only on numidic mountains. Such is the case for *Juniperus sabina*, *Alopecurus gerardii*, *Anthyllis montana*, *Scabiosa crenata*, *Daphne oleoides*, *Sedum majellense*, *Saponaria depressa*, *Euphorbia luteola*, *Campanula trichocalycina*, *Robertia taraxacioides*. Their

placement is probably more recent than that of the oro-endemics of the Atlas, and their migration by the Sicilian-Tunisian bridge in the Pleistocene is likely.

II.2.1.5—*Eastern Mediterranean Taxa.*—Eastern Mediterranean taxa include 160 species representing about 4% of the flora. Of course the eastern Mediterranean element is especially prominent in Libya and in Egypt where it is represented by such genera as *Sarcopoterium* and *Thymbra*, but especially by annual species belonging to the genera *Silene*, *Erysimum*, *Trifolium*, *Trigonella*, and *Verbascum*.

II.2.1.6—*Circum-Mediterranean Taxa.*—Circum-Mediterranean taxa represent the largest group (after the endemics) with 873 species and nearly 22% of the entire flora. It is unnecessary to dwell on this group, which correlates almost exactly with the entire flora from the point of view of family and generic representation.

However, a group of species should be pointed out which is included here, but which in fact show an element of the Mesogean type. Their distribution area stretches from the Atlantic to the western Himalaya. Among these species, most belong to orophilous lines. Their distribution resembles that of the genus *Cedrus* (Fig. 2). In particular may be noted: *Fraxinus xanthoxyloides*, *Prunus prostrata*, *Cotoneaster nummularia*, and *Scutellaria orientalis* (Quézel, 1957; Meusel, 1971).

Because of the age of their disjunction, these species are polymorphic. Indeed, this type of distribution is found especially in the endemo-vicariants series (cf. below).

II.2.2—*The Irano-Turanian Taxa*

There are hardly more than 30 Irano-Turanian taxa (without counting the endemics which belong to this biogeographical subdivision). This weak representation certainly confirms the absence of this region in North Africa and especially on the high plateaus of the Maghreb. It is nevertheless interesting to note that it is the Chenopodiaceae which have the greatest number of species belonging to this element. In particular may be noted: *Kochia prostrata*, *Anabasis aphylla*, *Noaea mucronata*, *Salsola paletzkiana*.

II.2.3—*Saharo-Arabian Taxa*

A little more than 120 species (3%) of the flora represent the Saharo-Arabian element in Mediterranean Africa. These species are not particularly interesting biogeographically. They nearly always represent southern infiltrations into the most arid part of the Mediterranean region of Hodna in Algeria and into the middle valley of the Moulouya in Morocco.

II.2.4—*Taxa of Northern Origin*

Among the Northern taxa are included the Atlantic (63, 1.5%), European and Eurasian (528, 13.1%), Paleotemperate (74, 1.8%), and Circumboreal (40, 1%) taxa. Without going into detail, the predominance of European and Eurasian taxa may be noted. These make up a large contingent which is commonly

FIGURE 2. Distribution of circum-Mediterranean taxa.

found in the wettest zones of the North African tells, particularly at the edge of water and in forest associations. Among the most noteworthy genera are: *Cyperus*, *Scirpus*, *Juncus*, *Salix*, *Ranunculus*, *Papaver*, *Fumaria*, *Sedum*, *Potentilla*, *Geranium*, *Acer*, *Anthriscus*, *Oenanthe*, *Caucalis*, and *Veronica*.

A certain number of orophilic species also belong to this group; the most representative are (without counting the phenomenon of microendemism): *Calamagrostis argentea*, *Agrostis alpina*, *Avena montana*, *Blysmus compressus*, *Aquilegia vulgaris*, *Aconitum lycoctomum*, *Draba tomentosa*, *Rhamnus pumilla*, *Meum athamanticum*, *Androsace villosa*, *Gentiana verna*, *Euphrasia minima*, *Galium pumilum*, and *Asperula odorata*.

The circumboreal element, although weakly present, also appears mostly on high mountains, the Atlas in particular, and, by its presence, poses interesting historical problems. As I have shown (Quézel, 1957), this element generally represents the vestiges of a flora which came into North Africa at the glacial periods and which arrived almost exclusively by way of the Iberian Peninsula, perhaps bird dispersal playing a small role. Among the most noteworthy representatives are: *Botrychium lunaria*, *Dryopteris lonchitis*, *Nardus stricta*, *Polygonum bistorta*, *Carex capillaris*, *Luzula spicata*, *Luzula multiflora*, *Cerastium cerastioides*, *Sagina saginoides*, *Viola palustris*, *Gentiana tenella*, and *Parnassia palustris*.

The Atlantic element is especially well represented in Morocco, but it is also found along the Algero-Tunisian coast. Among the most notable types are the genera: *Chaeturus*, *Airopsis*, *Antinoria*, *Periballia*, *Gratiola*, *Illecebrum*, and *Quercus pyrenaica*.

II.2.5—*Taxa of Tropical Origin*

It is appropriate to expand somewhat on the tropical taxa, particularly within the framework of a total floristic and biogeographical interpretation of the African continent.

According to the figures, they represent a small group in Mediterranean

Africa (excluding the Nile Delta) with about 55 species and 1.3% of the flora. Without considering here the problem of Mediterranean endemics of tropical origin, a study of Table 3 shows immediately that two families alone contain more than half of these species: the Gramineae (24) and the Cyperaceae (8). In fact, an even higher number could be envisaged if one takes into account many of them which are connecting (?) Sudano-Angolan-Mediterranean species.

Among the latter, many correspond to hygrophytes, or even hydrophytes, whose presence in Mediterranean Africa can be linked to transport by migratory birds (at least for some of them). There are in particular, and mainly for the marshes of the Moroccan or Calle coast, several representatives of the genera *Cyperus* (*C. michelianus*, *C. polystachyos*, *C. corymbosus*), *Fimbristylis* (*F. squarrosa*, *F. dichotoma*), as well as *Rhynchospora alba*, *Fuirena pubescens*, *Polygonum senegalense*, *Typha elephantina*, *Oldenlandia capensis*, *Laurenbergia tetrandra*, *Glinus lotoides*, and *Alternanthera sessilis*.

Numerous annuals linked to cultivation and without great biogeographical interest can also be noted here; they belong principally to the genera: *Sorghum*, *Digitaria*, *Brachiaria*, *Paspalum*, *Paspalidium*, *Echinochloa*, *Panicum*, *Eragrostis*, *Dactyloctenium*, and *Achyranthes aspera*.

Indeed, the most remarkable group is made up of species generally present both in the tropical dry zone and in the Mediterranean region where they are often abundant. They pose an interesting biogeographical problem. The Gramineae and, in particular the Andropogoneae, play a major role here. Most of these probably arrived in the Mediterranean region during the Quaternary pluvial periods. Their path of migration followed the mountain chains adjacent to the Red Sea, but also the high Saharan mountains, and even the Atlantic coast. Among the most noteworthy are (cf. Fig. 3): *Chrysopogon aucheri*, *Andropogon distachyus*, *Hyparrhenia hirta*, *Heteropogon contortus*, *Themeda triandra*, *Trichholaena teneriffae*, *Cenchrus ciliaris*, *Pennisetum setaceum*, *Enneapogon scaber*, *Oropetium africanum* (Gillet & Quézel, 1959), *Dichanthium annulatum*, as well as on the Moroccan coast, *Enteropogon rupestris*.

II.3—ENDEMISM IN MEDITERRANEAN AFRICA

Successively we shall look at generic and specific endemism and then try to define the biogeographical significance of endemism in the flora of Mediterranean Africa.

II.3.1—*Generic Endemism*

In spite of several taxonomic uncertainties, it is clear that generic endemism is relatively important in Mediterranean Africa, and especially in the Maghreb. In fact 38 genera can be put into this category, although some, which are present in the Mediterranean region, are more widely represented in the Saharan region, and will be studied later on. These are principally the genera *Oudneya*, *Eremophyton*, *Perralderia*, *Rhanterium*, *Warionia*, and *Tourneuxia*.

Among the remaining 32 genera: 12 belong to the Cruciferae: *Trachystoma*,

TABLE 3. The principal biogeographical elements of the families of Mediterranean Africa. Heading abbreviations are as follows: Gen. = Genera, Sp. = Species, End. = Endemics, N.A. = North African, I.-M. = Ibero Mauritanian, Mac. = Macaronesian, W.-Med. = Western Mediterranean, E.-Med. = Eastern Mediterranean, Med. = Mediterranean, I.-T. = Irano-Turanian, S.-S. = Saharo-Sindian, Atl. = Atlantic, E.&E. = European & Eurasian, Pt. = Paleotemperate, Cb. = Circumboreal, Trop. = Tropical, Oth. = Other.

Family	Gen.	Sp.	End.	N.A.	I.-M.	Mac.	W.-Med.	E.-Med.	Med.	I.-T.	S.-S.	Atl.	E.&E.	Pt.	Cb.	Trop.	Oth.
Acanthaceae	1	2	.	.	.	.	.	1	1	.	.	.	.	.	.	.	.
Aceraceae	1	4	.	.	.	.	.	.	1	.	.	.	3	.	.	.	.
Adoxaceae	1	1	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.
Aizoaceae	6	11	2	.	.	.	.	1	1	.	.	.	.	4	.	.	3
Alismataceae	3	4	.	.	.	.	1	.	.	.	.	2	.	.	.	.	1
Amaranthaceae	4	11	.	.	.	.	.	.	.	1	1	.	.	2	.	.	7
Amaryllidaceae	8	20	4	1	4	.	3	.	5	.	.	1	.	.	.	1	1
Anacardiaceae	2	7	1	.	.	1	.	.	4	1	.	.	.	.	.	.	.
Apocynaceae	2	4	.	.	.	.	1	.	3	.	.	.	.	.	.	.	.
Aquifoliaceae	1	1	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.
Araceae	6	8	1	.	.	.	1	.	6	.	.	.	.	.	.	.	.
Araliaceae	1	1	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.
Aristolochiaceae	1	4	.	.	1	.	1	.	2	.	.	.	.	.	.	.	.
Asclepiadaceae	6	11	2	.	1	1	.	1	4	.	1	.	1	.	.	.	.
Balanophoraceae	1	1	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.
Berberidaceae	3	4	1	.	1	.	.	2	.	.	.	.	.	.	.	.	.
Betulaceae	2	2	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.
Boraginaceae	26	86	23	.	1	1	6	8	26	.	7	.	4	1	2	1	.
Butomaceae	1	1	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.
Buxaceae	1	2	.	.	1	.	.	.	1	.	.	.	.	.	.	.	.
Callitrichaceae	1	3	.	.	.	.	.	.	.	.	.	.	2	.	.	.	1
Campanulaceae	9	37	16	.	6	.	3	2	3	.	.	.	6	.	.	.	1
Capparaceae	2	5	1	.	1	.	.	.	1	.	1	.	.	.	.	1	.
Caprifoliaceae	3	11	1	.	1	.	2	.	8	.	.	.	3	.	.	.	.
Caryophyllaceae	32	227	75	.	28	1	20	9	38	1	11	2	25	2	3	.	12
Celastraceae	2	2	.	.	.	.	.	.	1	.	.	.	.	.	.	1	.
Ceratophyllaceae	1	2	.	.	.	.	.	.	.	.	.	.	1	.	.	.	1
Chenopodiaceae	19	28	8	1	3	2	2	1	11	5	7	.	5	.	.	.	13
Cistaceae	5	60	11	2	13	2	11	2	16	.	3	.	.	.	.	.	.

TABLE 3. *Continued.*

Family	Gen.	Sp.	End.	N.A.	I.-M.	Mac.	W.-Med.	E.-Med.	Med.	I.-T.	S.-S.	Atl.	E.&E.	Pt.	Cb.	Trop.	Oth.
Cneoraceae	1	1	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.
Commelinaceae	1	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Compositae	106	563	231	5	63	5	52	6	96	2	22	3	45	1	4	2	27
Convolvulaceae	5	31	8	.	1	.	4	2	6	.	.	.	2	1	.	.	7
Coriariaceae	1	1	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.
Cornaceae	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Crassulaceae	5	43	13	.	6	.	1	3	9	.	.	1	9	.	.	1	.
Cruciferae	84	215	72	2	21	2	12	10	40	4	7	2	32	1	1	.	9
Cucurbitaceae	3	3	.	.	.	.	.	.	1	1	.	.	1	.	.	.	.
Cupressaceae	3	7	.	.	.	.	2	.	3	.	.	.	.	2	.	.	.
Cyperaceae	9	80	.	.	1	.	1	1	5	.	.	2	23	4	4	8	27
Dioscoreaceae	1	1	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.
Dipsacaceae	6	24	7	1	2	.	3	2	2	2	.	.	5	.	.	.	.
Droseraceae	1	1	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.
Elatinaceae	1	3	.	.	.	.	.	.	.	.	.	1	1	1	.	.	.
Ephedraceae	1	5	.	1	.	.	.	1	3	.	.	.	.	.	.	.	.
Ericaceae	3	9	.	.	2	.	3	.	2	.	.	1	.	.	1	.	.
Euphorbiaceae	5	62	13	4	7	1	9	4	9	.	4	2	7	.	.	1	2
Fagaceae	2	8	1	.	2	.	1	3	.	.	.	1	.	.	.	.	.
Frankeniaceae	1	6	1	2	.	.	.	1	1	.	.	1	.	.	.	.	.
Gentianaceae	6	16	3	.	.	.	.	.	7	.	.	1	2	1	2	.	.
Geraniaceae	2	47	17	.	4	.	3	2	12	.	1	1	7	.	.	.	.
Gramineae	114	338	42	10	20	.	21	12	89	.	14	8	51	20	1	24	32
Grossulariaceae	1	3	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.
Haloragidaceae	2	4	.	.	.	.	.	.	.	.	.	.	1	.	2	.	1
Hippuridaceae	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hydrocharitaceae	3	3	.	.	.	.	.	.	.	.	.	.	1	.	.	.	2
Hypericaceae	1	24	2	.	2	1	2	2	10	.	.	1	3	1	.	.	.
Illecebraceae	1	1	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.
Iridaceae	5	32	9	.	8	.	3	.	8	.	3	1	.	.	.	.	.

TABLE 3. *Continued.*

Family	Gen.	Sp.	End.	N.A.	I.-M.	Mac.	W.-Med.	E.-Med.	Med.	I.-T.	S.-S.	Atl.	E.&E.	Pt.	Cb.	Trop.	Oth.
Juglandaceae	1	1	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.
Juncaceae	2	29	1	.	1	.	2	.	5	.	.	1	9	4	1	1	4
Juncaginaceae	1	4	.	.	.	.	.	.	1	.	.	.	.	.	.	.	3
Labiatae	34	222	99	8	32	.	19	4	33	.	1	.	21	2	1	.	2
Lauraceae	1	1	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.
Leguminosae	49	432	105	4	61	3	43	21	146	3	10	3	31	2	.	.	.
Lemnaceae	3	5	.	.	.	.	.	.	.	.	.	.	.	1	.	.	4
Lentibulariaceae	2	5	.	.	.	.	.	.	.	.	.	1	2	1	.	1	.
Liliaceae	24	113	25	1	9	1	15	8	37	2	1	1	12	1	.	.	.
Linaceae	3	18	7	.	1	.	3	1	4	.	.	.	2	.	.	1	.
Loranthaceae	2	3	.	.	.	.	.	.	1	.	.	.	1	1	.	.	.
Lythraceae	2	8	.	.	1	.	.	.	4	.	.	.	1	.	.	.	2
Malvaceae	6	32	6	.	5	.	1	2	11	.	1	1	4	.	.	.	1
Menyanthaceae	1	1	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.
Monotropaceae	1	1	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.
Moraceae	1	1	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.
Myrtaceae	1	1	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.
Najadaceae	1	5	1	.	.	.	.	.	.	.	.	.	.	.	.	1	3
Nyctaginaceae	2	2	1	.	.	.	.	.	.	.	.	.	.	1	.	.	.
Nymphaeaceae	2	2	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.
Oleaceae	5	6	.	.	.	.	.	.	4	.	.	.	2	.	.	.	.
Onagraceae	6	14	3	.	.	.	.	.	1	.	.	1	1	2	1	2	3
Orchidaceae	13	54	5	.	.	.	5	.	20	.	.	.	24	.	.	.	.
Orobanchaceae	2	40	9	1	5	.	3	1	8	.	2	1	9	.	.	1	1
Oxalidaceae	1	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3
Paeoniaceae	1	1	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.
Palmae	2	2	.	.	.	.	1	.	.	.	1	.	.	.	.	.	.
Papaveraceae	11	52	11	1	11	.	3	4	9	.	.	.	10	.	.	1	2
Parnassiaceae	1	1	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.
Phytolaccaceae	1	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2

TABLE 3. *Continued.*

Family	Gen.	Sp.	End.	N.A.	I.-M.	Mac.	W.-Med.	E.-Med.	Med.	I.-T.	S.-S.	Atl.	E.&E.	Pt.	Cb.	Trop.	Oth.
Pinaceae	3	6	1	1	1	.	.	.	3	.	.	.	.	.	.	.	.
Plantaginaceae	2	23	4	1	.	.	3	.	8	.	1	.	5	.	1	.	.
Plumbaginaceae	5	46	17	3	5	.	6	.	6	1	3	5	.	.	.	.	.
Polygalaceae	1	7	3	.	1	.	1	.	2	.	.	.	.	.	.	.	.
Polygonaceae	3	36	5	1	.	.	1	.	5	.	3	1	6	1	1	1	11
Portulacaceae	2	2	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1
Posidoniaceae	1	1	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.
Potamogetonaceae	1	12	.	.	.	.	.	.	.	.	.	.	1	3	.	.	8
Primulaceae	9	16	2	.	.	.	1	1	3	.	.	2	5	.	2	.	.
Punicaceae	1	1	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.
Pyrolaceae	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Rafflesiaceae	1	1	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.
Ranunculaceae	13	64	10	.	2	.	6	2	14	1	.	2	19	5	.	.	3
Resedaceae	4	25	11	.	3	.	1	.	1	3	1	.	.	.	3	1	1
Rhamnaceae	3	8	.	.	.	.	2	.	4	.	.	.	2	.	.	.	.
Rosaceae	19	60	6	.	6	.	3	2	9	1	1	1	28	1	2	.	.
Rubiaceae	9	50	8	4	5	.	3	1	17	.	.	1	9	1	.	1	.
Ruppiaceae	1	2	.	.	.	.	.	.	1	.	.	.	.	.	.	.	1
Rutaceae	2	4	1	.	1	.	.	.	2	.	.	.	.	.	.	.	.
Salicaceae	2	10	.	.	.	.	.	.	1	1	.	.	8	.	.	.	.
Sambucaceae	1	2	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.
Santalaceae	2	6	2	.	1	.	.	.	3	.	.	.	.	.	.	.	.
Sapindaceae	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Sapotaceae	1	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Saxifragaceae	2	18	7	.	4	.	2	3	.	.	.	.	2	.	.	.	.
Scrophulariaceae	18	145	50	9	21	.	11	22	.	.	5	3	16	2	4	1	.
Selaginaceae	1	3	2	.	.	.	.	.	1	.	.	.	.	.	.	.	.
Solanaceae	9	18	1	.	4	.	.	1	3	.	1	.	3	.	.	1	4
Sparganiaceae	1	1	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.
Tamaricaceae	2	10	.	2	1	.	1	1	.	.	3	1	.	1	.	.	.
Taxaceae	1	1	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.
Theligonaceae	1	1	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.

TABLE 3. *Continued.*

Family	Gen.	Sp.	End.	N.A.	I.-M.	Mac.	W.-Med.	E.-Med.	Med.	I.-T.	S.-S.	Atl.	E.&E.	Pt.	Cb.	Trop.	Oth.
Thymelaeaceae	2	17	4	2	4	.	.	.	4	.	1	.	2	.	.	.	.
Trapaceae	1	2	.	.	.	.	.	.	.	.	.	.	.	1	.	1	.
Typhaceae	1	3	.	.	.	.	.	.	.	.	.	.	.	.	.	1	2
Ulmaceae	2	2	.	.	.	.	.	.	1	.	.	.	1	.	.	.	.
Umbelliferae	61	183	53	9	21	5	12	7	38	2	2	5	28	1	.	.	.
Urticaceae	3	8	.	.	1	.	.	1	3	.	1	.	2	.	.	.	.
Vahliaceae	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Valerianaceae	4	26	4	2	3	.	2	2	10	.	.	1	2	.	.	.	.
Verbenaceae	3	5	.	.	.	.	.	.	2	.	.	.	.	.	.	.	3
Violaceae	1	10	4	.	.	.	.	.	2	.	.	.	3	.	1	.	.
Vitaceae	1	1	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.
Zannichelliaceae	2	2	.	.	.	.	.	.	1	.	.	.	.	.	.	.	1
Zosteraceae	1	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2
Zygophyllaceae	6	10	3	.	.	1	1	.	.	2	2	.	.	.	.	1	.
TOTALS	916	4034	1038	78	408	27	321	160	873	33	122	63	528	73	40	56	214
PERCENTAGES			25.76	1.93	10.13	0.57	7.97	3.97	21.68	0.81	3.00	1.56	13.11	1.83	0.99	1.36	5.31

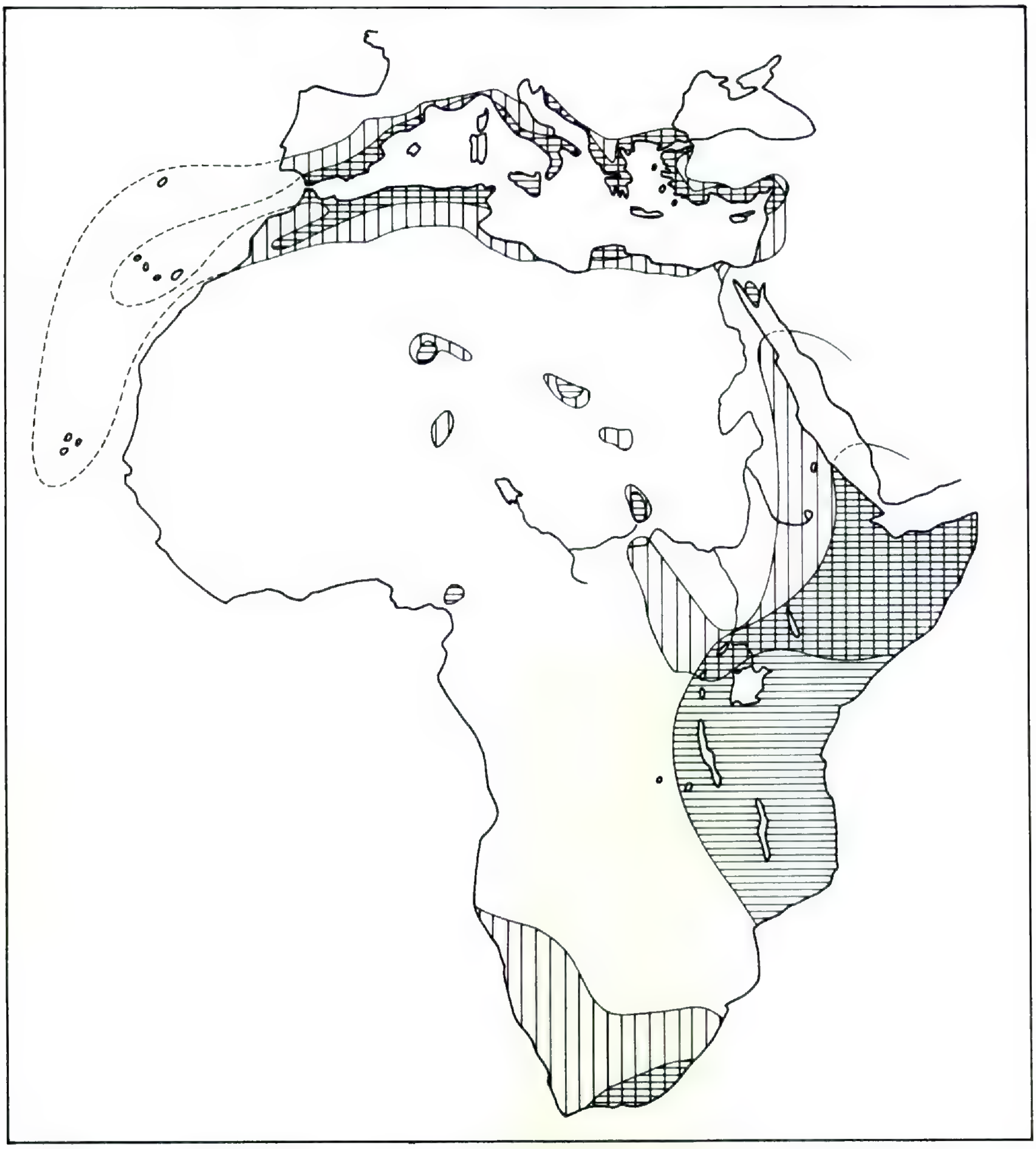

FIGURE 3. Distribution of *Hyparrhenia hirta* (vertical lines) and *Andropogon distachyus* (horizontal lines).

Raffenaldia, *Hemicrambe*, *Cordylocarpus*, *Fezia*, *Kremeriella*, *Muricaria*, *Crambella*, *Otocarpus*, *Ceratocnemum*, *Rhytidocarpus*, and *Psychine*; 4 to the Compositae: *Fontquera*, *Anvilleina*, *Lifago*, and *Mecomiscus*; 3 to the Umbelliferae: *Sclerosiadium*, *Pachyctenium*, and *Balansaea*; 4 to the Leguminosae: *Hesperolaburnum*, *Argyrocytisus*, *Lyauteya*, and *Benedictella*; 2 to the Gramineae: *Libyella* and *Agropyropsis*; to the Labiateae: *Saccocalyx* and *Pitardia*; and to the Chenopodiaceae: *Oreobliton* and *Traganopsis*. Finally there is an endemic genus in the following families: Liliaceae (*Battandiera*), Amaryllidaceae (*Hannonia*), Sapotaceae (*Argania*), and Campanulaceae (*Feeria*).

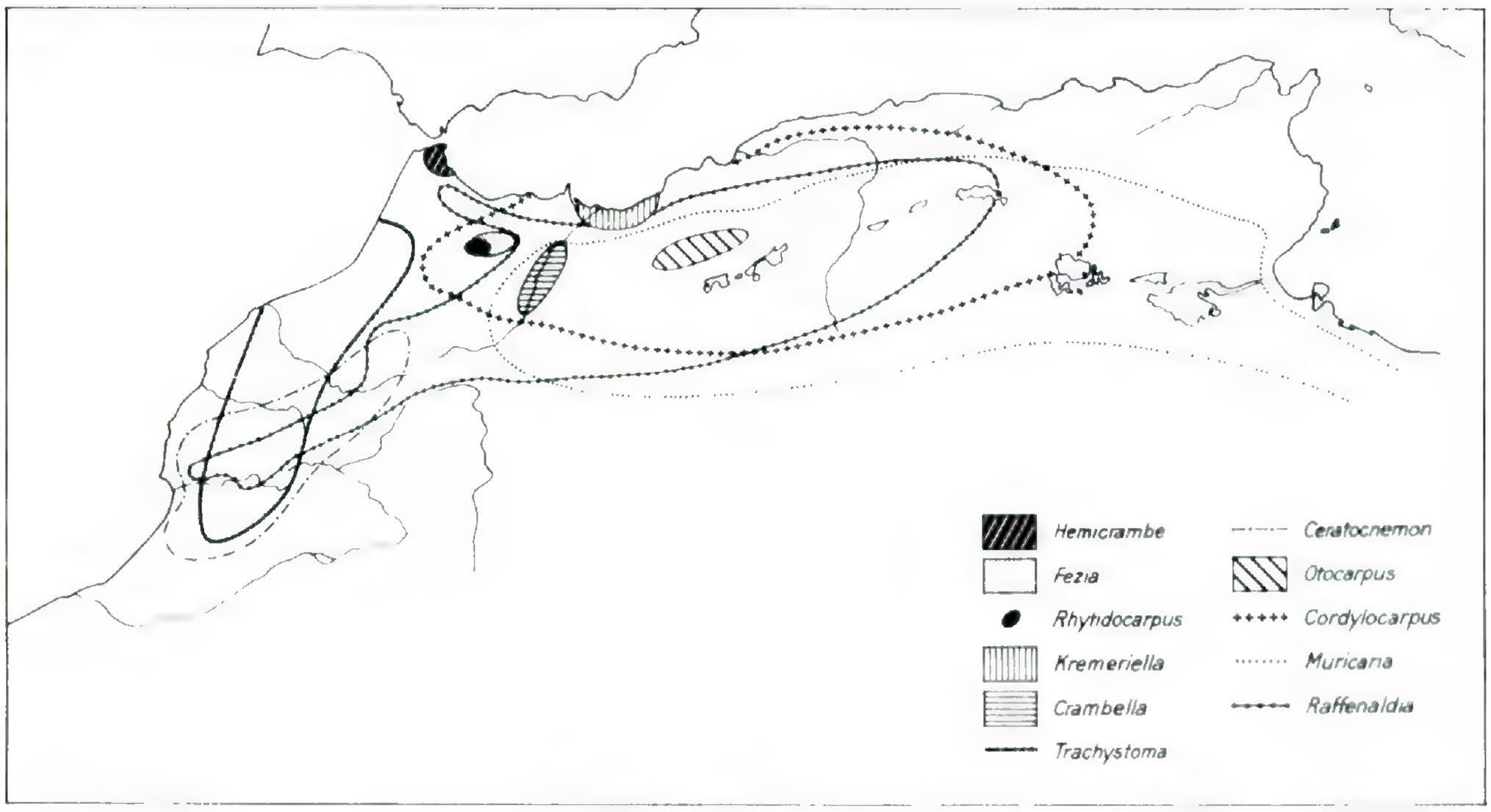

FIGURE 4. Distribution of endemic genera of Cruciferae in Mediterranean North Africa. *Psychine* occurs nearly throughout Mediterranean North Africa.

Most of these genera are monospecific and have a restricted distribution (cf. Fig. 4). However, *Trachystoma* has three species and *Raffenaldia*, *Pitardia* and *Mechomiscus* have two species.

Certainly, the most remarkable characteristic is the real generic proliferation which appears in the Maghreb in the Cruciferae.

Among the other genera, some are certainly related to other North African or Mediterranean genera; others, on the other hand, represent paleoendemic elements. Among the former are *Anvilleina*, *Lifago*, *Libyella*, *Agropyropsis*, *Saccocalyx*, *Traganopsis*, *Battandiera*, whose links with the genera *Anvillea*, *Filago*, *Mibora*, *Agropyron*, *Thymus*, *Traganum* and *Ornithogalum* are evident.

II.3.2—*Specific Endemism*

Of the some 925 genera inventoried in this work for Mediterranean Africa, about 330, or 30%, have endemic species. It would be too lengthy to enumerate these species here, but it is nevertheless interesting to learn something about the genera having the largest number of endemic species. I have not gone beyond four endemic species per genus: 48: *Silene*; 34: *Centaurea*, 25: *Teucrium*; 23: *Linaria*; 18: *Astragalus*, *Thymus*; 16: *Ononis*, *Euphorbia*; 15: *Erodium*; 14: *Limonium*; 13: *Bupleurum*, *Leucanthemum*, *Crepis*; 12: *Sedum*, *Genista*, *Campanula*; 11: *Reseda*, *Echium*, *Marrubium*, *Stachys*, *Atractylis*; 10: *Vicia*, *Celsia*; 9: *Sideritis*, *Carthamus*, *Carduncellus*; 8: *Romulea*, *Helianthemum*, *Galium*, *Orobanche*, *Anacyclus*, *Chrysanthemum*, *Senecio*; 7: *Fumaria*, *Arabis*, *Saxifraga*, *Adenocarpus*, *Cytisus* (sensu lato), *Lotus*, *Linum*, *Convolvulus*, *Salvia*, *Micromeria*, *Onopordum*, *Leontodon*, *Taraxacum*; 6: *Festuca*, *Scilla*, *Allium*, *Rumex*, *Spergularia*, *Ranunculus*, *Diplotaxis*, *Alyssum*, *Hedysarum*, *Lavatera*, *Eryngium*,

Carum, Odontites, Phagnalon, Andryala; 5: *Arenaria, Buffonia, Lathyrus, Daucus, Valerianella, Scabiosa, Verbascum, Scrophularia, Plantago, Armeria, Thymelaea, Pulicaria, Filago, Anthemis, Cirsium, Launaea*; 4: *Avena, Cynosurus, Atriplex, Delphinium, Brassica, Potentilla, Viola, Bunium, Pituranthos, Ferula, Lavandula, Calamintha, Origanum, Evax, Calendula, Artemisia, Hypochoeris, Picris, Hieracium.*

Without going into a biogeographical interpretation, it is nevertheless appropriate to point out that nearly all of these genera are unquestionably of Mediterranean origin; the only notable exceptions are *Saxifraga, Festuca, Ranunculus, Avena, Potentilla, Viola, Cirsium* and *Hieracium*, more generally Eurasian or Holarctic, *Artemisia* and *Atriplex*, better developed in the Irano-Turanian Region, and *Pituranthos*, of Saharan origin.

II.3.3—*Biogeographical Significance of Endemic Taxa*

It is impossible to study here in detail the biogeographical significance of the 1,037 endemic species inventoried in Mediterranean Africa; it is nevertheless interesting to clarify at least some points.

II.3.3.1—*Endemics of Mediterranean Origin.*—These represent more than 80% of the total. Among these, more than a third are related to genera essentially circum-Mediterranean, the principal ones being: *Asphodelus, Scilla, Brassica, Diplotaxis, Arabis, Reseda, Sedum, Ononis, Trifolium, Lavatera, Ferula, Cyclamen, Globularia, Teucrium, Salvia, Sideritis, Stachys, Campanula, Evax, Anacyclus, Anthemis, Chrysanthemum*, and *Centaurea.*

The genera more specifically Western Mediterranean are perhaps even better represented by: *Catapodium, Romulea, Spergularia, Silene, Hedysarum, Helianthemum, Erodium, Eryngium, Bupleurum, Echium, Linaria, Odontites, Solenanthus, Armeria, Limonium, Lavandula, Thymus, Filago, Calendula, Atractylis, Carthamus*, and *Carduncellus.*

Among the genera of Ibero-Mauritanian origin, endemics are present in *Leucojum, Vagaria, Rupicapnos, Adenocarpus, Lafuentia, Brachyapium.*

Inversely, the endemics belonging to the genera *Bellevalia, Tunica, Astragalus, Cicer, Pterocephalus, Rindera, Micromeria* are more generally of Eastern Mediterranean origin.

Since a biogeographical and taxonomic interpretation is already nearly complete, (Quézel, 1957, 1964a), we shall not discuss it at length. However, we would still like to emphasize a certain number of points.

II.3.3.2—*Endemics of North African Origin.*—Along with the endemic genera mentioned above, one should point out the existence of endemic sections in the genera *Agropyron* (*Goulardiopsis* by *A. embergeri*), *Draba* (*Helicodraba* by *D. hederifolia* and *Acrodraba* by *D. oreadum*), *Phagnalon* (*Gnaphaliopsis* by *P. helichrysoides, P. platyphyllum, P. embergeri* and *P. iminouakense*), *Cyclamen* (*Dodecatheoides* by *C. rohlfsianum*).

Some genera also have some very distinctive species in North Africa. Such is the case for the hardy *Cynosurus* (*C. peltieri, C. balansae*, and *C. junceus*), for the shrubby *Polygala* (*P. balansae, P. webbiana*, and *P. munbyana*), the

Adenocarpus with umbelliform inflorescences (*A. umbellatus*, *A. faurei*, and *A. segonei*) and also the *Buffonia perennes* group.

II.3.3.3—*The Mountain Endemics.*—The North African mountains (Quézel, 1957) contain one of the most remarkable concentrations of endemic taxa in North Africa; in fact, there are about 170 on the high Moroccan Atlas. A large number of these endemics belong to genera or to groups of species of orophytes which are circum-Mediterranean, or even Mesogean. These emphasize the strict affinities existing in the original plant population of the mountains of the Mediterranean periphery. A few examples are (Fig. 5) the representatives of the genera *Cedrus* and *Abies*, as well as *Cicer atlanticum*, a very exact vicariant of *C. incisum* of Greece and of the Near East, and of *C. minutum* of Ebourouz. There are many other examples in the genera *Minuartia*, *Silene*, *Potentilla*, *Astragalus*, *Viola*, *Hypericum*, *Sideritis*, *Marrubium*, *Veronica*, *Asperula*, *Pterocephalus*, *Rindera*, *Campanula*, and *Leuzea*.

II.3.3.4—*Endemics of Northern Origin (in the broad sense).*—Although these are not very numerous, they are of some interest. Even though the migration to North Africa of species of northern origin generally appears recent and, for the most part, concomitant with glaciations (the nearly total absence of specific endemism proves it clearly), some noteworthy exceptions point to the possibility of a much older migration. Thus it is that the genus *Gentiana* is represented on the high Atlas by two endemic species, one of which (*G. tornezyana*) is the type of the section *Pseudotricha*, and the other (*G. atlantica*) belongs to an orophilous southern European lineage absent, however, from the Alps.

Other examples are the following: *Agrostis atlantica*, vicariant of *A. rupestris*; *Luzula atlantica*, related to *L. graeca*; representatives of the genera *Erigeron* and *Gnaphalium*, also related to European or Anatolian species. Still in the Atlas, *Aster pujosii*, vicariant of *A. amellus* and *A. willkommii*, can be linked to the element of Sarmatic origin. Some endemics of northern origin are found in North Africa, especially on the eastern Algerian coast at low altitudes. Their presence there seems to be very old. Such is the case for *Digitalis atlantica*, *Pedicularis numidica*, *Lysimachia cousiniana*, *Epimedium parralderianum*, *Epilobium numidicum*, *Galium numidicum*, related specifically and respectively to *D. ambigua*, *P. silvatica*, *L. nemorum*, *E. pubigenum*, *E. parviflorum* and *G. mollugo*.

Coronilla atlantica and *Doronicum atlanticum*, as well as the *Teucrium* endemics of the *Scorodonia* section, have a comparable significance, but a wider distribution.

II.3.3.5—*Endemics of Irano-Turanian and Saharo-Arabian Origin.*—These endemics are not numerous. However, endemics of Irano-Turanian origin are, probably, *Zygophyllum cornutum*, *Anabasis prostrata*, as well as various representatives of the genus *Artemisia* (particularly *A. atlantica*, *A. mesatlantica*, and *A. ifranensis*) whose affinities with *A. herba-alba* are evident. The same applies to the genus *Hohenackeria* (*H. polyodon*).

The only endemic species of Saharan origin found within the limits of the Mediterranean region appears to be *Fagonia harpago* of the southern face of the Anti-Atlas.

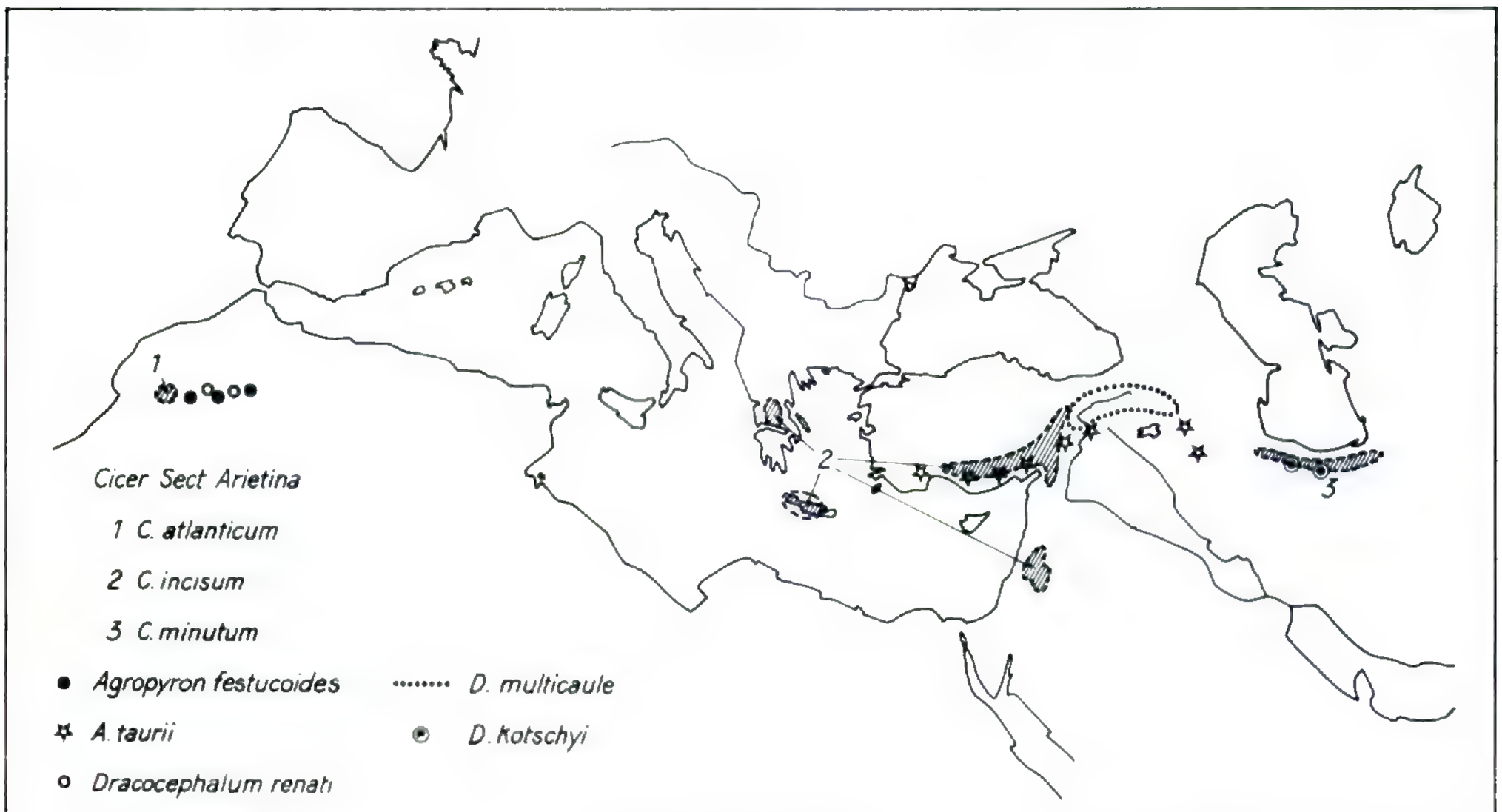

FIGURE 5. Distribution of North African mountain endemics.

II.3.3.6—*Endemics of Tropical Origin.*—Although not numerous in Mediterranean Africa (about 15), these are nevertheless noteworthy from several points of view. First, it is relevant to note that the largest number of them is found in southern Morocco, especially in the Macaronesian section of this country. In fact, most also have vicariants in the Canaries or could be integrated, if necessary, into the Macaronesian element. Specific examples are *Acacia gummifera*, *Commelina rupestris*, *Boerhaavia maroccana*, *Kalanchoe faustii*, *Leptochloa ginae*, and *Pentzia hesperidum*, all the only representatives of these genera in Mediterranean Africa.

Among the other endemic species of tropical African origin that are widespread in North Africa are two representatives of the genus *Hertia* (*H. cheirifolia* and *H. maroccana*), and of the genus *Caralluma* (*C. hesperidum* and *C. joannis*), as well as *Polycarpaea akkensis*, *Andrachne maroccana*, and *Cleome amblyocarpa*.

The genera *Lotononis* (with 3 endemic species in Morocco) and *Argyrolobium* (2 species) are also of tropical African origin. *Trichodesma calcaratum* and *Withania adpressa* are found in the Sahara, but are otherwise found mainly in Mediterranean Africa.

The relatively large representation of endemics of tropical origin in southern Morocco is well known, but merits attention. Indeed, their presence is certainly old in this zone and points to the possibilty of floristic exchanges between the Mediterranean and tropical regions, certainly since the Tertiary and probably even before the Saharan aridification (cf. below). The continued presence of these species, often quite rare as well, has been conditioned by the local climate and essentially by the high degree of atmospheric humidity. It should be pointed out that the coast of the Red Sea must have played an analogous role even

though endemism there is scarcely perceptible for tropical taxa which, in any case, are not found in the Mediterranean region.

II.3.3.7—*Endemics of Macaronesian Origin.*—Macaronesian endemics occur of course, mainly in the Macaronesian Moroccan region whose essential physiognomic element is *Argania spinosa*. However, this tree, as well as several other species, spread more or less widely into the Mediterranean region, and notably into the oceanic Sahara. The endemic elements most representative are *Euphorbia echinus*, *Senecio antheuphorbium*, *Bubonium imbricatum*, *Aizoon theurkauffii*, *Limonium beaumierianum*, *L. tuberculatum*, *Limoniastrum ifniense*, *Lotus pseudo-creticus*, *L. simonae*, and *Frankenia chevallieri*.

In Algeria, at Bejaïa, *Bupleurum plantagineum* also appears to belong to this group. In fact it is close to *B. salicifolium* of the Canaries and of Madeira, but also to *B. dumosum* of the Ida or Tanana of western Morocco.

II.3.4—*The Geographical Aspect of Endemism in Mediterranean Africa*

It is evident that the Maghreb alone is the basic reservoir for the endemic species. In fact, of some 1,037 species cited, almost a thousand are found there.

No estimate is made here of the number of endemic species in each of the countries of the Maghreb since this does not correspond to any geographical reality. Nevertheless, this count has been made for Algeria (Quézel, 1964b), where about 250 endemic species exist. Recently Lecompte-Barbet (1975) made this study for Morocco, but she clearly gives too broad a meaning to this term at the taxonomic level (she includes subspecies in her totals) as well as at the geographical level. Therefore it is difficult to estimate from these results what the actual specific endemism of Morocco is; numbers on the order of 600–650 are likely.

A very special case which deserves attention is that of the Cyrenaic Mediterranean, which has very distinctive characteristics and a certain influence of eastern Mediterranean elements in the makeup of its endemic ancestry. It is difficult to calculate the exact number, but it is probably more than 40. Among those unquestionably having elements of eastern Mediterranean origin are: *Bellevalia cyrenaica*, *Allium* spp., *Arum cyrenaicum*, *Crocus boulosii*, *Ornithogalum barba-caprae*, *Athamantha della-cellae*, *Tunica daveana*, *T. marmarica*, *Astragalus cyrenaicus*, *A. taubertianus*, *Origanum cyrenaicum*, *Micromeria guichardii*, *M. fortii*, *Nepeta cyrenaica*, *Teucrium barbeyanum*, *T. davaeanum*, and *Arbutus pavarii*.

Other species are more typically of circum-Mediterranean origin. These are: *Avena beguinotiana*, *Cynosurus junceus*, *Orchis cyrenaica*, *Thesium erythronicum*, *Silene daveana*, *S. marmarica*, *Reseda odorata*, *R. pampaniniana*, *Sedum mirum*, *S. bracteatum*, *Medicago cyrenaica*, *Convolvulus mairei*, *Plantago phaeostoma*, *Onopordum cyrenaicum*, *Libyella cyrenaica*, *Cyclamen rohlfsianum*, *Viola scorpiuroides*, and *Pachyctenium mirabile*.

Egypt, on the contrary (excluding Sinai), has only a small number of endemic species in its Mediterranean portion. Noted may be: *Tunica compressa*, *Lotus polyphyllus*, *Ebenus armitagei*, and *Ferula marmarica*.

III—Saharan Africa

The vast desert zone stretching between Mediterranean Africa on the north and tropical Africa on the south, and for which we have previously indicated the boundaries, which is truly quite artificial, occupies approximately 7,000,000 km^2.

In this enormous territory, in spite of an usually extremely hostile climate, developed a flora of great importance, which is especially prevalent in the wettest areas: the northern and southern borders, the ocean shores, and in particular the mountain massifs. This flora presents many problems of biological and geobotanical significance, problems essentially related to the climatic history and especially to the recent climatic history of this area, where next to the eremitic autochthonous elements, an often significant number of Mediterranean and tropical elements appears. In fact, even if some of the eremetic elements are truly from the Sahara (in the actual sense of the term), others belong to the old African xerophytic flora usually called the "Rand Flora."

For all these reasons, the analysis of the flora presently occupying the Sahara is particularly delicate, but also very interesting and instructive!

III.1—the families

III.1.1—*Generic and Specific Richness* (Table 5)

For the entire Saharan region about 104 families of phanerogamic plants have been divided into several categories; for the vascular cryptogams about 10.

Concerning the generic representation, the hierarchy is as follows: 2 families contain more than 50 genera (Compositae 80 and Gramineae 74), 4 more than 20 (Cruciferae 44, Leguminosae 30, Chenopodiaceae 23, Caryophyllaceae 22), 7 more than 10 (Umbelliferae 18, Boraginaceae 17, Labiatae and Scrophulariaceae 16, Aizoaceae, Asclepiadaceae and Liliaceae 11). Fourteen families possess between 6 and 10 genera (Convolvulaceae, Cucurbitaceae, Euphorbiaceae and Rubiaceae 9, Cyperaceae, Malvaceae and Zygophyllaceae 8, Acanthaceae and Capparaceae 7, Amaranthaceae, Papaveraceae, Polygonaceae, Solanaceae and Verbenaceae 6). Thirty-seven families contain from 2 to 5 genera, and 37 are monospecific in the Saharan area.

In the vascular cryptogams, all of the Filicales embrace 11 genera, the other families (4) are represented by a single genus.

In species richness, only 3 families surpass 100 (Gramineae 203, Compositae 164, Leguminosae 154), 3 surpass the 50 mark (Cruciferae 73, Chenopodiaceae 64, Caryophyllaceae 73), and 14 families possess between 20 and 49 species (Scrophulariaceae 49, Cyperaceae 46, Boraginaceae and Zygophyllaceae 43, Euphorbiaceae 40, Malvaceae 38, Labiatae 36, Umbelliferae 35, Convolvulaceae 34, Aizoaceae 25, Asclepiadaceae and Capparaceae 23, Rubiaceae 22, Solanaceae 21). Fifteen families have between 10 and 19 species (Liliaceae 19, Polygonaceae 18, Geraniaceae, Papaveraceae and Tamaricaceae 15, Amaranthaceae and Cucurbitaceae 14, Cistaceae, Plantaginaceae and Resedaceae 13, Plumbaginaceae 12, Ranunculaceae 11, Acanthaceae, Juncaceae and Potamogetonaceae 10). In

addition 21 families possess from 5 to 9 species. Four species are found in 3 families, 3 in 7, and 2 in 15. Finally, 21 families are represented in the Sahara by only a single species.

III.1.2—*Biogeographical Significance at the Family Level*

Let me emphasize immediately, that contrary to what happened in Mediterranean Africa, the families offer very diverse biogeographical significance. Later on I will return to this question which is one of the fundamental aspects of the Saharan flora, but it is, however, interesting to emphasize that the tropical element is in the majority in a large number of families. Particularly to be noted are the following: Acanthaceae, Aizoaceae, Amaranthaceae, Asclepiadaceae, Burseraceae, Capparaceae, Commelinaceae, Convolvulaceae, Cucurbitaceae, Elatinaceae, Euphorbiaceae, Leguminosae, Lythraceae, Malvaceae, Menispermaceae, Moraceae, Nyctaginaceae, Pedaliaceae, Sapindaceae, Solanaceae, Sterculiaceae, Tiliaceae, Vahliaceae, Verbenaceae, and Vitaceae. Such is still the case for the Avicenniaceae, Balanitaceae, Combretaceae, Ebenaceae, Moringaceae, Rhizophoraceae, and Salvadoraceae, all represented by a single species in the Sahara.

The Saharan element (sensu lato) dominates in the Boraginaceae, Chenopodiaceae, Compositae, Cruciferae, Frankeniaceae, Plumbaginaceae, Resedaceae, Tamaricaceae, and Zygophyllaceae.

The Mediterranean element dominates in the Araceae, Caryophyllaceae, Ephedraceae, Geraniaceae, Labiatae, Orobanchaceae, Papaveraceae, Plantaginaceae, Rhamnaceae, Santalaceae, and Umbelliferae.

Finally, it may be noted that Polygonaceae, Ranunculaceae, and Salicaceae predominately exhibit the Irano-Turanian element, although this phenomenon is not particularly significant except perhaps for the Polygonaceae. With the Juncaceae, Najadaceae, and Potamogetonaceae, the cosmopolitan species or those with a very vast area of distribution are dominant.

III.1.3—*Endemic Richness at the Family Level*

One must emphasize at the beginning the considerable impoverishment in endemic species that can be observed in the Sahara in comparison to Mediterranean Africa. The total percentage of endemics is no more than 11.6%, in contrast to 25.7% in Mediterranean Africa.

One single family shows more than 20 endemic species (Leguminosae 21) and 6 more than 10 (Gramineae 19, Caryophyllaceae, Compositae and Umbelliferae 13, Cruciferae 12, and Zygophyllaceae 10). Three show from 5 to 10 (Scrophulariaceae 7, Euphorbiaceae and Plumbaginaceae 5). There are 4 endemic species in the Asclepiadaceae, Boraginaceae, Cistaceae, Labiatae and Rubiaceae, 3 in the Aizoaceae, Dipsacaceae, Ephedraceae, Liliaceae, Papaveraceae and Polygonaceae, and 2 in the Chenopodiaceae, Convolvulaceae, Cyperaceae, Gentianaceae, Hypericaceae, and Resedaceae. Finally, Apocynaceae, Crassulaceae, Cupressaceae, Elatinaceae, Frankeniaceae, Geraniaceae, Malvaceae, Moraceae, Myrtaceae, Nyctaginaceae, Oleaceae, Onagraceae, Plantaginaceae,

TABLE 4. Distribution of the total number of species in Saharan Africa into its biogeographical subdivisions.

Subdivision	Number	Percentage %
Number of genera	617	
Number of species	1,6_0	
Endemics (sensu lato)	190	11.6
Saharo-Arabian	359	22.7
Irano-Turanian	75	4.5
Mediterranean (sensu lato)	344	21.2
Tropical (sensu lato)	524	32.3
Cosmopolitan or plurilocal and others	126	7.7

Polygalaceae, Primulaceae, Ranunculaceae, Rosaceae, Solanaceae, Tamaricaceae, and Verbenaceae possess only one.

It is notable that in the Sahara, 51 families do not possess endemic species, estimated at a rough guess to be half of the families present.

III.1.4—*The Global Biogeographical Spectrum*

In order not to excessively complicate an often controversial question, I only consider the Saharo-Arabian, Irano-Turanian, and Mediterranean elements, and some of tropical origin, in Table 4 and make further analyses in the text. The simple analysis of this spectrum (Table 4) and its comparison with that which has been obtained for Mediterranean Africa (Table 2) shows numerous peculiarities:

For a surface at least seven times greater, the number of species is almost three times poorer, whereas the number of genera remains relatively high (615 instead of 916).

The endemic element which represents more than 25% of the flora in Mediterranean Africa here reaches scarcely 12%.

While in Mediterranean Africa there occurs an overwhelming predominance of the Mediterranean element (46% without counting the endemics which would make it closer to 65%), in the Sahara, on the contrary, there is a nearly equal partition between Saharo-Arabian (22.7%), Mediterranean (21.2%) and tropical (32%) elements.

These peculiarities not only confirm the biogeographical heterogeneity of the Sahara but also the hostility of the ecological conditions which now prevail there and which are only reflections of the climatic cataclysms which have occurred there since the end of the Quaternary. Finally, it should be remembered that in the Sahara the major part of the flora is confined in the "massif refugia" or the "zones of safey," while very large surfaces are practically sterile.

III.2—THE PRINCIPAL BIOGEOGRAPHICAL ELEMENTS

We consider in succession the Saharo-Arabian, Irano-Turanian, Mediterranean, and tropical elements.

III.2.1—*Saharo-Arabian Taxa*

They belong to a large number of the families, but are in fact abundant only in the Boraginaceae (*Lappula*, *Echiochilon*, *Moltkia*, *Arnebia*, *Gastrocotyle*, *Megastoma*), the Caryophyllaceae (*Pteranthus*, *Sclerocephalus*, *Gymnocarpos*, *Paronychia*, *Polycarpaea*, *Silene*), the Chenopodiaceae (*Schanginia*, *Sevada*), the Compositae (*Launaea*, *Atractylis*, *Gymnarrhena*, *Lasiopogon*, *Iphiona*, *Pulicaria* (including *Frankoeria*), *Anvillea*, *Asteriscus*, *Rhetinolepis*, *Lasiospermum*, *Chlamydophora*), the Cruciferae (*Reboudia*, *Farsetia*, *Savignya*, *Moricandia*, *Pseuderucaria*, *Notoceras*, *Morettia*, *Zilla*, *Schouwia*, *Anastatica*, *Robeschia*, *Torularia*, *Schimpera*, *Eremobium*), the Gramineae [*Aristida* (p.p.), *Schismus*, *Desmostachya*, *Boissiera*], the Leguminosae (*Trigonella*, *Lotus*, *Astragalus*, *Alhagi*), the Rubiaceae (*Gaillonia*), the Resedaceae (*Reseda*), the Tamaricaceae (*Tamarix*), the Umbelliferae (*Pituranthos*, *Ammodaucus*) and the Zygophyllaceae (*Zygophyllum*, *Fagonia*, *Nitraria*). If a great number of the genera cited above correspond in fact to some elements with Saharo-Mediterranean or Mediterranean-Saharan connections, they nevertheless occupy an appreciable, indeed an important, place in the Saharan flora, and they comprise a large number or reasonably large number of the species with an essentially Saharan or Saharo-Arabian distribution.

III.2.2—*Irano-Turanian Taxa*

Although few, they merit being cited; they appear especially in the eastern Sahara, but some are widespread over most of the Sahara. Let us point out: the Liliaceae (*Bellevalia*, *Leopoldia*), the Salicaceae (*Populus euphratica* and *Salix subserrata*), the Salsolaceae (*Halocnemum*, *Salsola*, *Seidlitzia*, *Hammada*, *Noaea*), the Leguminosae (*Astragalus*), the Malvaceae (*Alcea*), the Umbelliferae (*Astoma*, *Ducrosia*, *Zosima*), the Boraginaceae (*Paracaryum*), Plantaginaceae (*Plantago*), and the Compositae (*Atractylis*, *Zoegea*, *Artemisia*).

III.2.3—*Mediterranean Taxa*

Mediterranean taxa are relatively numerous, as I have noted, and appear (cf. Table 5) among numerous families (especially Caryophyllaceae, Compositae, Cruciferae, Gramineae, Leguminosae, Papaveraceae, Plantaginaceae, Rubiaceae, Scrophulariaceae, Umbelliferae). Their significance is quite variable.

Some appear only in the northern Sahara immediately adjacent to their Mediterranean range and have only a minor biogeographical value. Others are usually located close to areas with water, or are clearly anthropophilous [*Juncus*, *Scirpus*, *Polypogon*, *Ranunculus*, *Trigonella*, *Medicago*, *Trifolium*, *Frankenia* (p.p.), *Apium*, *Torilis*, *Centaurium*, *Galium*, *Plantago*, *Picris*, *Scorzonera*, *Lactuca*].

Others, on the other hand, represent isolated colonies, persisting due to relatively favorable ecological conditions, and constituting for the most part vestiges of a flora much more widely spread in the Sahara at the time of the rainy Quaternary periods. The most remarkable case is that from the high Saharan

TABLE 5. The principal biogeographical elements of the families of Saharan Africa. Heading abbreviations are as follows: Gen. = Genera, Sp. = Species, End. = Endemics, S.-A. = Saharo-Arabian, I.-T. = Irano-Turanian, Med. = Mediterranean, Eur. = European, Trop. = Tropical, Oth. = Other.

Family	Gen.	Sp.	End.	S.-A.	I.-T.	Med.	Eur.	Trop.	Oth.
Acanthaceae	7	10	.	.	.	.	.	10	.
Aizoaceae	11	25	3	1	.	1	.	20	.
Amaranthaceae	6	14	.	1	1	.	.	7	5
Amaryllidaceae	1	5	.	3	.	.	.	1	1
Anacardiaceae	2	5	.	.	1	2	.	2	.
Apocynaceae	3	3	1	.	.	1	.	1	.
Araceae	2	2	.	.	.	2	.	1	.
Asclepiadaceae	11	23	4	4	.	3	.	12	.
Avicenniaceae	1	1	.	.	.	.	.	1	.
Balanitaceae	1	1	.	.	.	.	.	1	.
Balanophoraceae	1	1	.	.	.	1	.	.	.
Boraginaceae	17	43	4	17	2	5	.	14	1
Burseraceae	1	2	.	.	.	.	.	2	.
Campanulaceae	4	9	.	4	.	4	.	1	.
Capparaceae	7	23	.	1	.	1	.	21	.
Caryophyllaceae	22	63	13	13	.	26	.	7	4
Celastraceae	1	1	.	.	.	.	.	1	.
Chenopodiaceae	23	64	2	39	6	8	.	.	9
Cistaceae	1	13	4	7	.	2	.	.	.
Combretaceae	1	1	.	.	.	.	.	1	.
Commelinaceae	3	8	.	.	.	.	.	8	.
Compositae	80	164	13	62	7	44	.	32	5
Convolvulaceae	9	34	2	4	2	2	.	20	4
Crassulaceae	2	3	1	.	.	1	.	1	.
Cruciferae	44	73	12	32	3	23	.	2	1
Cucurbitaceae	9	14	.	1	.	1	.	12	.
Cupressaceae	2	2	1	.	.	1	.	.	.
Cyperaceae	8	46	2	1	.	4	.	25	14
Dipsacaceae	2	6	3	1	.	2	.	.	.
Ebenaceae	1	1	.	.	.	.	.	1	.
Elatinaceae	2	5	1	.	.	.	.	4	.
Ephedraceae	1	8	3	.	.	5	.	.	.
Ericaceae	1	1	.	.	.	.	.	.	1
Euphorbiaceae	9	40	5	12	2	5	.	16	.
Frankeniaceae	1	6	1	3	.	2	.	.	.
Gentianaceae	4	7	2	.	.	2	.	1	2
Geraniaceae	3	15	1	4	.	7	.	3	.
Gramineae	74	203	19	29	2	50	.	76	27
Hydrocharitaceae	5	6	.	.	.	.	.	4	2
Hypericaceae	1	4	2	.	.	2	.	.	.
Juncaceae	2	10	.	.	.	3	.	.	7
Labiatae	16	36	4	5	.	18	.	7	2
Leguminosae	30	153	22	32	7	25	.	66	1
Lemnaceae	1	2	.	.	.	.	.	.	2
Lentibulariaceae	1	2	.	.	.	.	.	1	1
Liliaceae	11	19	3	4	4	6	.	2	.
Linaceae	1	1	.	.	.	1	.	.	.
Loranthaceae	.	.	.	.	.	.	.	.	.

TABLE 5. *Continued.*

Family	Gen.	Sp.	End.	S.-A.	I.-T.	Med.	Eur.	Trop.	Oth.
Lythraceae	3	8	.	.	.	1	.	7	.
Malvaceae	8	32	1	.	3	5	.	23	.
Menispermaceae	2	2	.	.	.	.	.	2	.
Moraceae	1	6	1	.	.	1	.	4	.
Moringaceae	1	1	.	.	.	.	.	1	.
Myrtaceae	1	1	1	.	.	.	.	.	.
Najadaceae	1	3	.	.	.	.	.	.	3
Neuradaceae	1	1	.	1	.	.	.	.	.
Nyctaginaceae	2	9	1	.	.	.	.	8	.
Nymphaeaceae	1	2	.	.	.	.	.	2	.
Oleaceae	2	4	1	.	.	.	.	3	.
Onagraceae	3	6	1	.	.	1	.	3	1
Orchidaceae	1	1	.	.	.	1	.	.	.
Orobanchaceae	2	9	.	1	.	4	.	1	3
Oxalidaceae	1	2	.	.	.	.	.	1	1
Palmae	3	3	.	1	.	.	.	2	.
Papaveraceae	6	15	3	1	4	7	.	.	.
Pedaliaceae	3	3	.	.	.	.	.	3	.
Plantaginaceae	1	13	1	2	3	7	.	.	.
Plumbaginaceae	3	12	5	5	.	1	.	1	.
Polygalaceae	1	3	1	.	.	.	.	2	.
Polygonaceae	6	18	3	2	7	4	.	.	2
Pontederiaceae	1	1	.	.	.	.	.	1	.
Portulacaceae	1	1	.	.	.	.	.	.	1
Potamogetonaceae	1	10	1	.	.	.	.	1	8
Primulaceae	3	3	1	.	.	.	.	.	2
Ranunculaceae	5	11	1	.	6	2	.	.	2
Resedaceae	5	13	2	7	.	2	.	2	.
Rhamnaceae	4	6	.	1	1	3	.	1	.
Rhizophoraceae	1	1	.	.	.	.	.	1	.
Rosaceae	3	4	1	.	2	.	.	.	.
Rubiaceae	9	22	4	1	1	8	.	8	1
Ruppiaceae	1	1	.	.	.	.	.	.	1
Rutaceae	1	1	.	1	.	.	.	.	.
Salicaceae	2	2	.	.	2	.	.	.	.
Salvadoraceae	1	1	.	.	.	.	.	1	.
Santalaceae	2	2	.	.	.	2	.	.	.
Sapindaceae	2	2	.	.	.	.	.	2	.
Sapotaceae	1	1	.	.	.	1	.	.	.
Scrophulariaceae	16	49	7	8	1	14	.	15	4
Selaginaceae	1	1	.	1	.	.	.	.	.
Simaroubaceae	.	.	.	.	.	.	.	.	.
Solanaceae	6	21	1	3	.	3	.	8	6
Sterculiaceae	4	6	.	.	.	.	.	6	.
Tamaricaceae	2	15	1	11	2	1	.	.	.
Thymelaeaceae	1	1	.	.	.	1	.	.	.
Tiliaceae	3	9	.	.	.	.	.	9	.
Typhaceae	1	2	.	.	.	.	.	2	.
Umbelliferae	18	35	13	5	3	12	.	2	.
Urticaceae	3	6	.	3	1	.	2	.	.
Vahliaceae	1	2	.	.	.	.	.	2	.

TABLE 5. *Continued.*

Family	Gen.	Sp.	End.	S.-A.	I.-T.	Med.	Eur.	Trop.	Oth.
Valerianaceae	1	2	.	.	.	2	.	.	.
Verbenaceae	6	7	1	.	.	1	.	5	.
Vitaceae	2	2	.	.	.	.	.	2	.
Zannichelliaceae	2	5	.	.	.	.	.	3	2
Zygophyllaceae	8	43	10	25	2	.	.	6	.
TOTALS	617	1,620	190	359	75	344	2	524	126
PERCENTAGES			11.6	22.2	4.5	21.2	1.2	32.3	7.7

mountains (Quézel, 1965:220) where persist about 27 species common to Hoggar and Tibesti, 26 belonging to the central Saharan Massif, and 7 or 8 limited to Tibesti, beside some 25 species with a Saharo-Mediterranean connection, and a certain number of endemics of Mediterranean origin (cf. below).

Without repeating here this complete list, some especially remarkable species may be noted: *Ephedra major*, *Luzula atlantica*, *Carex distans*, *Osyris alba*, *Anethum graveolens*, *Clematis flammula*, *Pistacia atlantica*, *Rhus tripartitum*, *Nerium oleander*, and *Celsia longirostris*.

Another refugium for the Mediterranean elements is formed by the Atlantic coast where appear: *Asparagus altissimus*, *Osyris alba*, *Frankenia pulverulenta*, *F. corymbosa*, *Convolvulus fatmensis*, *Lycium intricatum*, *Rhus oxyacantha*, *Launaea arborescens*, *Periploca laevigata*, and *Phagnalon purpurascens*.

III.2.4—*Tropical Taxa*

These constitute, percentage-wise, the most prevalent element in the Sahara, which is not without interest for biogeographical interpretation. As I stated earlier, the southern portion of this desert is heavily populated by essentially tropical elements. Elsewhere, besides a basic group with a tropical background, which is present almost everywhere except in the northen Sahara, and which forms part of the landscape of "Savanes désertiques à Acacia-Panicum" (Maire, 1940), the tropical element appears also in the Sahara in certain preferential points and in particular on the southern slope of the Saharan mountains, but also on their Piedmont, where, as at Tibesti (Quézel, 1958), it can form a true enclave of Sahelian vegetation. The coastal links of the Red Sea in Egypt, as well as the valley and the delta of the Nile, also offer a rich procession of tropical species in a zone with a Saharan climate. All these factors explain the important development of the tropical element (sensu lato) in the Sahara. It is a appropriate to consider different assemblages in succession.

III.2.4.1—*Sahelian Taxa* (Fig. 6).—Sahelian taxa are certainly the most numerous. They are divided into many families, of which some hygrophiles (Avicenniaceae, Balanophoracae, Elatinaceae, Hydrocharitaceae, Rhizophoraceae) are especially common in Egypt. The landscape of desert savanna, and the Sahelian enclaves of the Saharan mountains are in principle richer in Sahelian elements as one progresses towards the south (under similar climatic conditions).

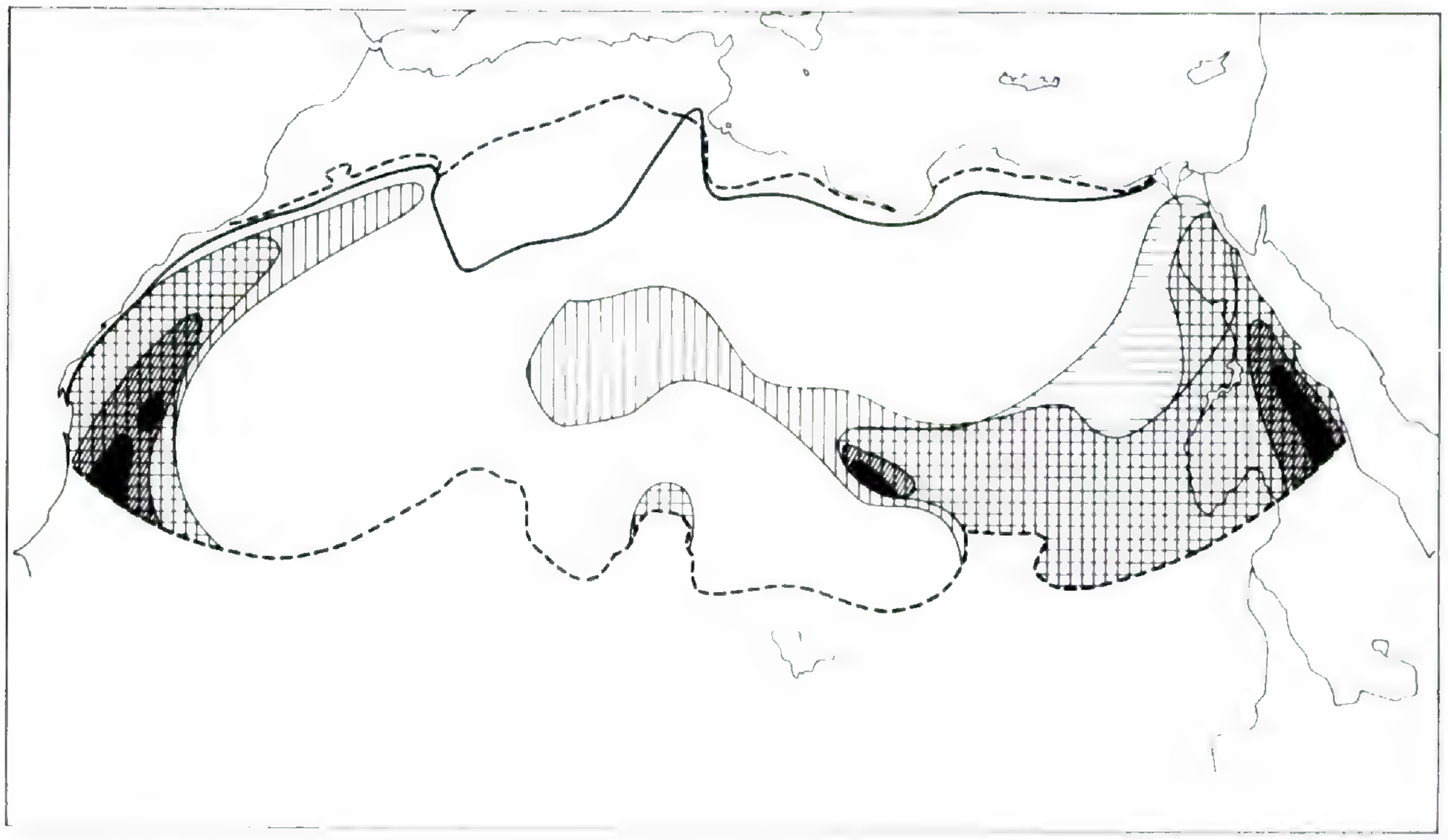

FIGURE 6. Distribution of Sahelian elements in Saharan Africa.—Heavy black line indicates the northern limit of *Acacia raddiana*.—Vertical lines indicate the area of distribution of *Balanites aegyptiaca* and *Moerua crassifolia*.—Horizontal lines indicate the area of *Capparis decidua*.—Diagonal lines indicate the area of the genus *Cadaba*.—Solid black indicates the area of *Boscia senegalensis*.

It is for this reason that the *Acacia raddiana* and *Ziziphus lotus* association of the northwestern Sahara possesses only 2.4% tropical elements while north of Hoggar, the *Panicum turgidum* and *Cassia aschreg* association reaches 12.6%, and further south, the *Cassia lanceolata* and *Tephrosia leptostachya* association reaches 39.9% (Quézel, 1965).

The valley and the delta of the Nile certainly represent a zone highly favorable to the development of the Sahelian taxa, as much as a result of local ecological conditions as a result of the permanent contribution of diaspores of African origin by the river, more particularly before the construction of the Aswan Dam.

From the floristic point of view and without entering into detail, the following families are best represented: Gramineae (with 40 genera and in particular, *Saccharum*, *Brachiaria*, *Cenchrus*, *Tragus*, *Latipes*, *Dinebra*, *Digitaria*, *Aristida*, *Sporobolus*, *Enneapogon*, *Eragrostis*), Leguminosae (*Crotalaria*, *Indigofera*, *Tephrosia*, *Sesbania*, *Taverniera*, *Rhynchosia*, *Cassia*, *Acacia*), Compositae (*Blumea*, *Conyza*, *Geigeria*, *Eclipta*), but also Aizoaceae (*Mollugo*, *Giesekia*, *Trianthema*), Capparaceae (*Capparis*, *Boscia*, *Cadaba*, *Maerua*, *Cleome*, *Crataeva*), Moringaceae, Vahliaceae, Burseraceae, Sapindaceae, Salvadoraceae, Tiliaceae (*Grewia*, *Corchorus*), Malvaceae (*Abutilon*, *Hibiscus*, *Sida*), Sterculiaceae, Combretaceae, Asclepiadaceae (*Calotropis*, *Glossonema*, *Oxystelma*, *Leptadenia*, *Pentatropis*), Boraginaceae (*Cordia*, *Trichodesma*), Verbenaceae, Scrophulariaceae (*Anticharis*, *Lindbergia*, *Sutera*, *Bacopa*, *Peplidium*), Acanthaceae (*Blepharis*, *Bar-*

leria, Peristrophe, Justicia, Ruellia, Monechma), and Pedaliaceae (*Sesamum, Pedalium, Rogeria*).

III.2.4.2—*African Highland Taxa.*—Highland taxa are abundantly prevalent in Tibesti, where besides endemic species which also belong there, it is appropriate to note miscellaneous ferns, specifically *Asplenium aethiopicum, Hypodematium crenatum*, but also *Acacia seyal, A. laeta, Ochradenus baccatus, Erhetia obtusifolia*, several *Ficus* species, *Hermannia abyssinica, Malhania ovata, Conyza abyssinica, Vernonia amygdalina*, as well as several species of *Abutilon* and *Convolvulus*. One must add to them *Satureia biflora, Silene kiliani*, present as well at Hoggar.

III.2.4.3—*Tropical Elements on Mountain Massifs Next to Coasts.*—The floristic inventory of the massifs adjoining the Atlantic, especially those which in Egypt border the Red Sea, demonstrates the appearance of a contingency important for tropical species, namely, the substitution of an increase in the rate of the atmospheric humidity, for infrequent, indeed almost total absence, of precipitation.

It is for this reason that numerous tropical genera appear on Zemmour, especially on the Adrar of Mauritania, which in general are present in the Sahara in the south (*Barleria, Blepharis, Peristrophe, Cleome, Combretum, Pluchea, Momordica, Bergia, Crotalaria, Indigofera, Tephrosia, Melhania, Bouchea*), but also *Tamarindus indica, Bauhinia rufescens, Jatropha*. However, this phenomenon remains quite limited.

In contrast on the shore of the Red Sea, and in particular towards the Sudanian frontiers, numerous tropical elements occur, which, besides some common types, include numerous elements belonging in general to some East African elements. Some 30 genera occur here which belong to this category. The most remarkable are, without a doubt, *Onychium, Sphaerocoma, Cometes, Puppalia, Psilotrichum, Taverniera, Delonix, Dodonea, Waltheria, Euclea, Enicostema, Jaubertia, Osteospermum, Aneilema*, and certainly not forgetting *Dracaena ombet*. Although this region is still situated in the Saharan climatic zone, it is difficult to integrate it into the Saharan phytogeographic domain.

III.2.4.4—*Elements of the tropical eremic flora or "Rand Flora."*—The existence of a xerophylic flora, indeed eremic of tropical origin, was, it seems, noted for the first time by Christ. It is Lebrum (1947) who named this group "Rand Flora," a term used again by Monod (1957) and by numerous others.

In spite of the implied unanimous accord presently existing on this question, the difficulty appears in fixing the exact boundaries of this flora which, theoretically, is found in the arid zones of tropical Africa both north and south. Many taxonomic uncertainties remain. It appears, however, possible to attribute to it several elements still present in the Canaries, such as cactoid *Euphorbia*, the genera *Caralluma* and *Dracaena*, and doubtlessly quite a large number of genera and species now present in the Sahara, such as: *Aristida* (p.p.), *Asthenatherum, Oropetium* (Fig. 7), *Enneapogon, Orygia, Cocculus, Neurada, Colocynthis, Monsonia, Ifloga, Caylusea, Oligomeris*, etc.

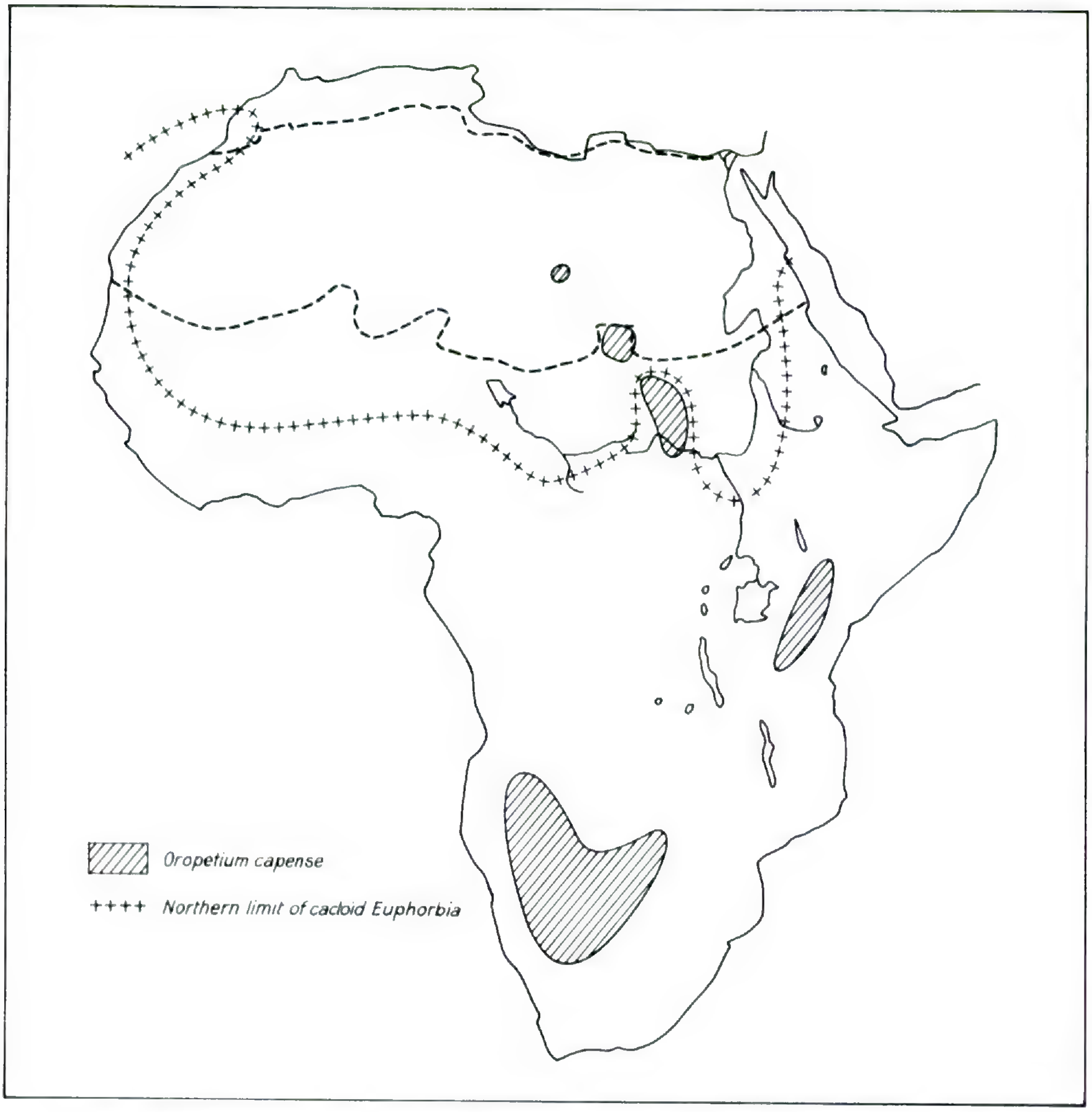

FIGURE 7. Distribution of several members of the tropical eremic flora or "Rand Flora."

III.2.5—*Pluro-Regional Elements*

In conclusion should be mentioned the existence in the Sahara of taxa with areas of distribution overlapping different biogeographical subdivisions and stretching in particular from tropical Africa, indeed southern Africa, to the Mediterranean region and finally perhaps quite close to the "Rand Flora." The case of the Gramineae, especially the Andropogoneae, alluded to earlier, can again be noted since these species are almost all present in the Sahara and in particular on the Saharan mountains. But it is advisable to cite several others (apart from hygrophilous or anthropophilous species without great significance), particularly *Commicarpus plumbagineus* and *Maytenus senegalensis*.

The same is true for *Erica arborea*, whose discovery in the Tibesti Massif (Bruneau de Miré & Quézel, 1959) was one of the greatest surprises furnished by the botanical exploration of this massif (Fig. 8).

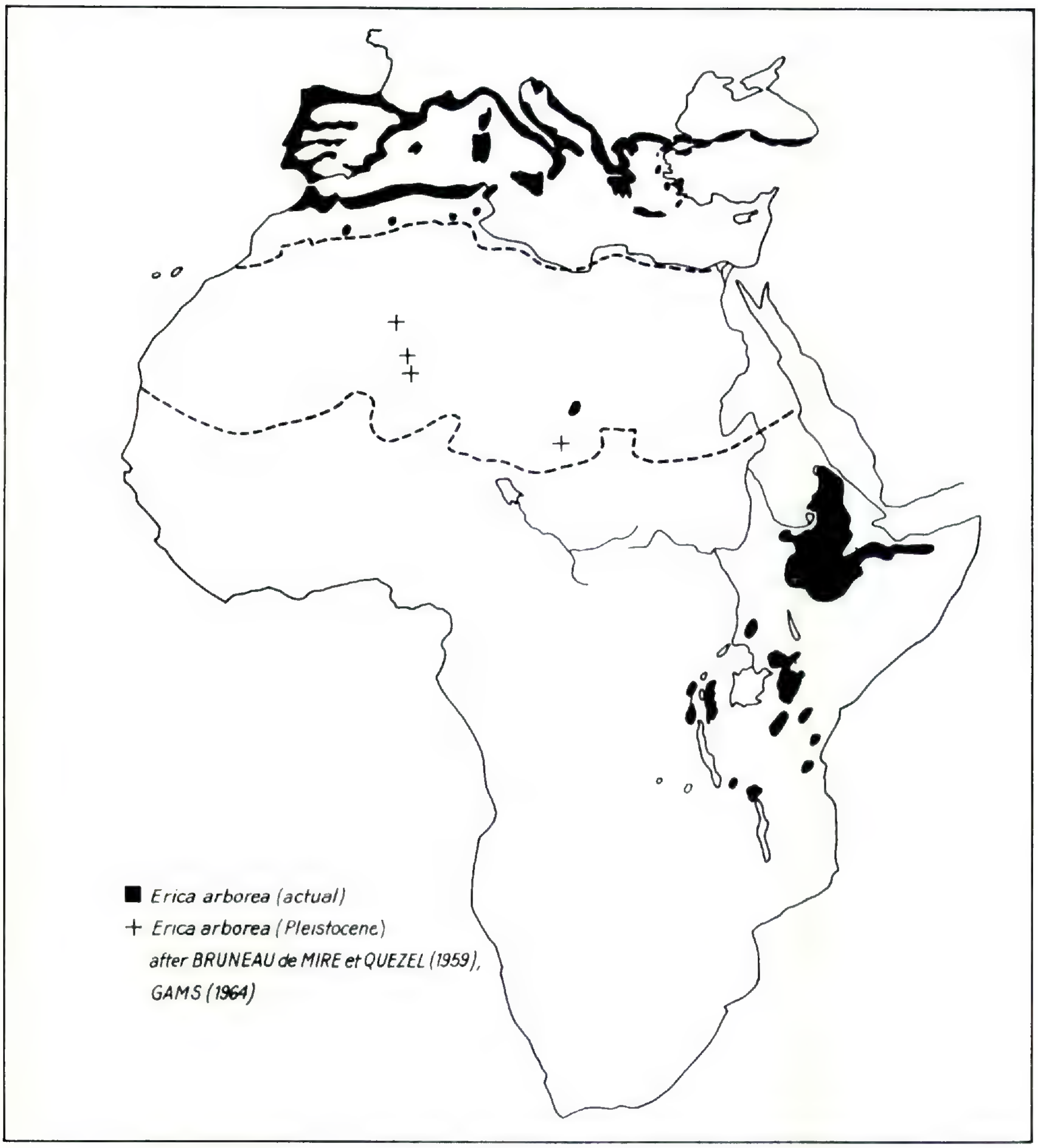

FIGURE 8. Distribution of *Erica arborea*; solid black indicates the present distribution, crosses indicate Pleistocene sites; after Bruneau de Miré & Quézel (1959), Gams (1964), and Straka (1970).

III.3—ENDEMISM IN THE SAHARA

III.3.1—*Generic Endemism*

Generic endemism in the Sahara (Quézel, 1964a) is clearly less developed than in Mediterranean Africa; only 16 genera can in fact be cited here, and some of them overlap more or less extensively into the Mediterranean region. It is remarkable to consider that for the entire subregion of the Sahara, it is the northwestern zone of the Sahara which is by far the richest in endemic genera

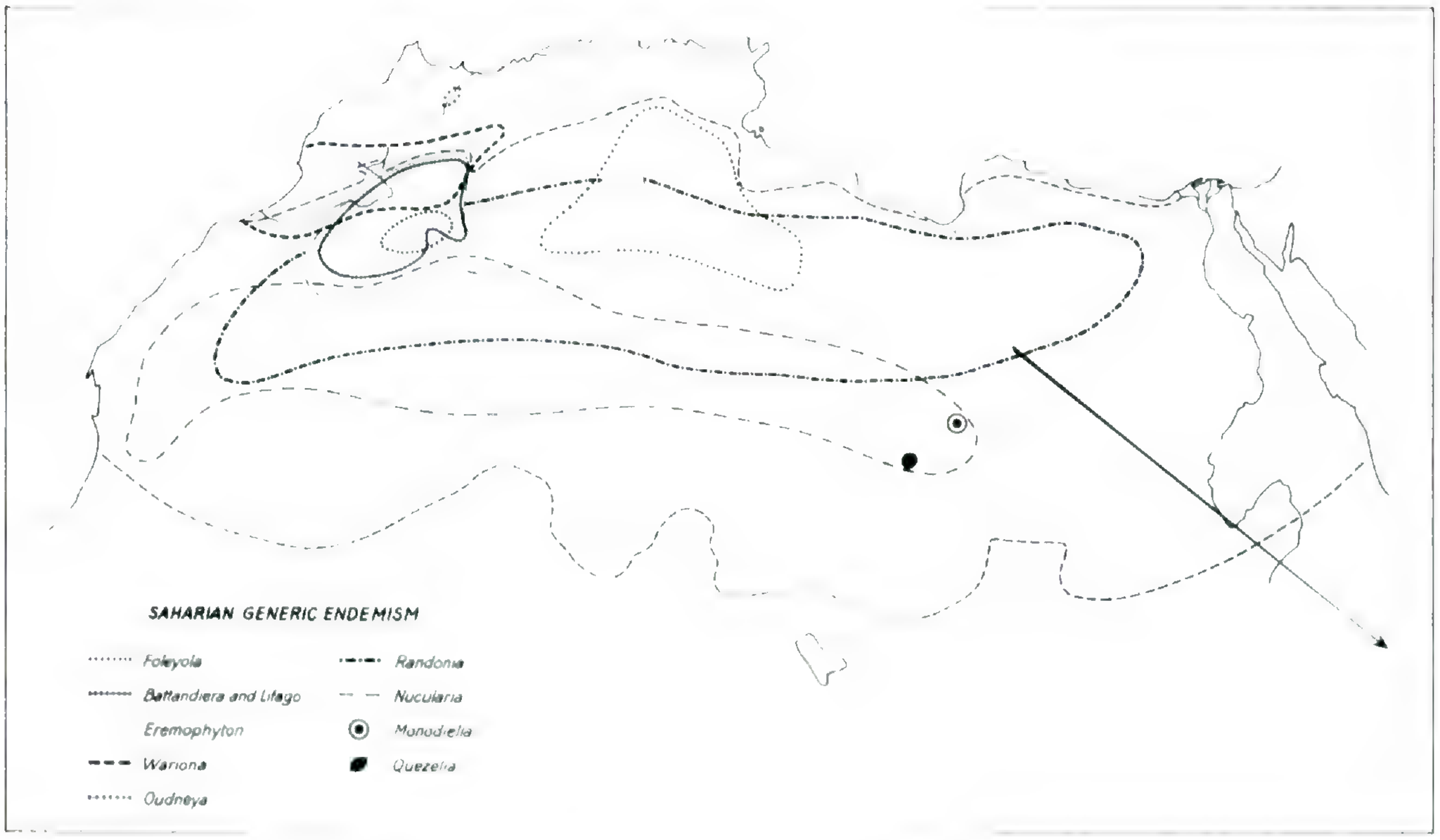

FIGURE 9. Distribution of endemic genera in the Sahara.

(Fig. 9). Indeed, *Battandiera*, *Lifago* and *Foleyola* are localized there and three others overlap more or less abundantly in this sector: *Eremophyton*, *Warionia*, and *Stephanochilus*.

The genera *Oudneya* and *Ammosperma* are south-Algerian-Moroccan in the major part of their distribution with one species, *O. zygarrhena*, in the Saharan enclave of the Moulouya valley.

Perralderia, *Tourneuxia*, *Rhanterium*, *Megastoma*, and *Nucularia* occupy much larger areas, but do not seem to spread into Libya towards the east. *Randonia*, on the other hand, reaches Egypt and Somaliland.

Finally, it is appropriate to note the rarest genera from Tibesti: *Mondiella* and *Quezelia*; the genus *Tibestina* has, however, been synonymized (Scholtz, 1974)

Indeed, of the 16 genera, some (*Stephanochilus*, *Lifago*) are even considered by some authors as mere sections (of the genera *Centaurea* and *Filago*). It is a question then of 6 Compositae, 5 Cruciferae, and only 1 representative of the Liliaceae, Chenopodiaceae, Boraginaceae, Gentianaceae, and Resedaceae.

Still of 16 genera, 14 are monospecific: *Battandiera*, *Lifago*, *Foleyola*, *Eremophyton*, *Warionia*, *Perralderia*, *Tourneuxia*, *Randonia*, *Rhanterium*, *Megastoma*, *Nucularia*, *Monodiella*, *Quezelia*, and *Stephanochilus*. The two others are bispecific.

All these genera are very diversified from the taxonomic viewpoint, and must certainly be associated with the paleoendemic element. The very small area occupied by some of them and the almost exclusive preponderance of monospecific types permit one to consider most of them as residual elements. Furthermore *Warionia* constitutes the only representative of the tribe Mutisiae.

III.3.2—*Specific Endemism*

Here again the remarkable fact is the very striking reduction of numbers of species in the heart of the Saharan flora. In spite of inherent difficulties with this question, we have cataloged 189 endemic species for the entire Saharan flora (Arabia excluded). This represents 11.9% of the entire flora as opposed to 25% in Mediterranean Africa.

The percentage of genera with endemic species is also lower in the Sahara (116 of 615 for 19%) than in Mediterranean Africa (330 of 925 for 37%).

It is also interesting to note the total disappearance in the Sahara of genera with high endemic rates; here only 8 genera have more than 4 endemic species. The generic representation of the endemism is the following: 6 endemic species: *Astragalus* and *Fagonia*; 4 endemic species: *Euphorbia*, *Ferula*, *Helianthemum*, *Phagnalon*, and *Zygophyllum*; 3 endemic species: *Bromus*, *Calligonum*, *Lotus* and *Silene*. Finally, 25 genera possess 2 endemic species and 78 a single one.

III.3.3—*Biogeographical Significance of Endemic Taxa*

Among the some 200 species which can be considered endemic in the territory of the Sahara a great number pose interesting problems, especially historical problems. Some will be examined later on.

III.3.3.1—*Endemics of Mesogean Origin.*—These endemics are indisputably the most numerous (about 90). They correspond both to endemics of Mediterranean origin and to those of Saharo-Arabian origin. It is necessary to note that it is often difficult to establish a precise limit between these two groups, and certain genera, indisputably of Mediterranean origin, have evolved some endemic species in the Sahara whose distribution is of the Saharan type. I will consider them, nevertheless, as endemics of Mediterranean origin.

Endemics of Mediterranean Origin.—Their list is long and I will discuss them as a function of their geographical distribution.

Some are found for the most part in the Sahara: *Koeleria rohlfsii*, *Diplotaxis acris*, *Lotus jolyi*, *L. roudairei*, *Astragalus akkensis*, *Euphorbia calyptrata*, *Megastoma pusillum*, *Antirrhinum ramosissimum*, *Atractylis aristata*, and *Volutaria leucantha*.

The northern Sahara to the south of the Maghreb offers: *Urginea noctiflora*, *Astragalus gombo*, *A. gombiformis*, *Genista saharae*, *Daucus biseriatus*, *Helianthemum eriocephalum*, *H. getulum*, *Euphorbia guyoniana*, *Convolvulus supinus*, *Anthemis sabulicola*, *Chrysanthemum macrocarpum*, *Pulicaria laciniata*, *Centaurea furfuracea*, *Stephanochilus omphalodes*, *Atractylis delicatula*, *A. carduus*, and *Heliotropium digynum*. The following species are, on the other hand, much more localized: *Atriplex mollis*, *Scabiosa camelorum*, *Astragalus kralikianus*, *Volutaria saharae*, and *Rupicapnos muricaria*.

The western Sahara has in its area: *Diplotaxis pitardiana*, *Moricandia foleyi*, *Convolvulus trabutianus*, *Withania adpressa*, *Ormenis eriolepis*, *O. lonadioides*, and *Atractylis babelii*.

In oceanic Sahara can be noted: *Lotus chalazei*, *Anethum foeniculoides*, *A.*

theurkhaufii, *Ephedra rollandii*, *Teucrium chardinianum*, and several species of *Limonium*.

In the eastern Sahara occur: *Dianthus guessfeldtianus*, *D. sinaicus*, *Biscutella elbensis*, *Meliotus serratifolia*, *Onosma galalense*, and *Pterocephalus aramicus*.

Some species belonging to the element with Saharo-Mediterranean connections can also be noted here; they are especially frequent in the northern half of the Sahara: *Reboudia erucarioides*, *Pseuderucaria teretifolia*, *Alyssum macrocalyx*, *Matthiola maroccana*, *Echium trigorrhizum*, *Marrubium desertii*, *Plantago akkensis*, *Senecio massaicus*, *Peralderia coronopifolia*, *Rhantherium suaveolens*, and several species of *Ferula*.

It is appropriate again to list under a special heading the remarkable endemics localized in the Saharan mountains.

Here may be noted *Olea laperrini*, *Cupressus duprezziana*, and *Myrtus nivellei* (Fig. 10). In fact, as we already indicated (Bruneau de Miré & Quézel, 1961), it is probable that the Saharan Olivier is linked with African sources. I will discuss this problem later. Belonging on this list from Hoggar and its extensions and from Tibesti are: *Verbascum dentifolium*; from Teffedest: *Astragalus geniorum*, *Helianthemum geniorum*; and from Tibesti: *Stipa tibestica*, *Celsia tibestica*, *Eragrostis kohorica*, *Foeniculum scoparium*, *Erodium oreophilum* and *Spergularia tibestica*, a local variant of *S. fontenellei* of Hoggar, where *Phagnalon garamantum* also appears.

Some other endemics localized in the mountainous areas are more likely associated with eastern Mediterranean sources: *Vartemia sericea* to *V. iphionoides*, *Campanula bordesiana* and *C. monodiana* with several Mideastern species.

Finally, although not endemics, several species with disjunct distributions merit being noted in this group. This is the case for *Erodium meynieri* and *Hypericum psilophytum* (south Morocco and the central Saharan Massif), *Centaurea touggourensis* (Hoggar and Bellezma), *Conyza triloba* (*Erigeron trilobus*) and *Senecio hoggariensis* (southern border of Maghreb, Hoggar, Tibesti, Sinai).

Endemics of Saharo-Arabian Origin.—They are clearly less numerous. Some genera, however, have evolved a certain number of taxa. The most remarkable belong to the Zygophyllaceae (Ozenda & Quézel, 1956), particularly *Fagonia* where, in spite of great difficulties of taxonomic rank, it seems possible to discern at least 6 endemic species, of which 3 are in the eastern Sahara; the genus *Zygophyllum* encompasses 4 endemic species, of which 2 are in oceanic Sahara (*Z. gaetulum* and *Z. waterlotii*). The genus *Calligonum* also has 3 endemic species of which 1, *C. azel*, with a wide distribution and the 2 others, *C. calvescens* and *C. arich*, are located between southern Tunisia and Tassili. Also included here is the genus *Limoniastrum* including, besides 1 Saharo-Mediterranean species (*L. guyonianum*), species occurring especially in the southern Morroco and in part of the Mediterranean regions (*L. feei*, *L. ifniensis*, *L. weygandiorum*). In the western Sahara the genus *Echiochilon* evolved *E. chazaliei* and *E. simmoneaui*. Finally, in the northern Sahara, we can note *Enarthrocarpus clavatus*, *Eremophyton chevalieri*, *Moricandia foleyi* among the crucifers and *Pituranthos battandieri* and *P. triradiatus* among the Umbelliferae. In the Chenopodiaceae

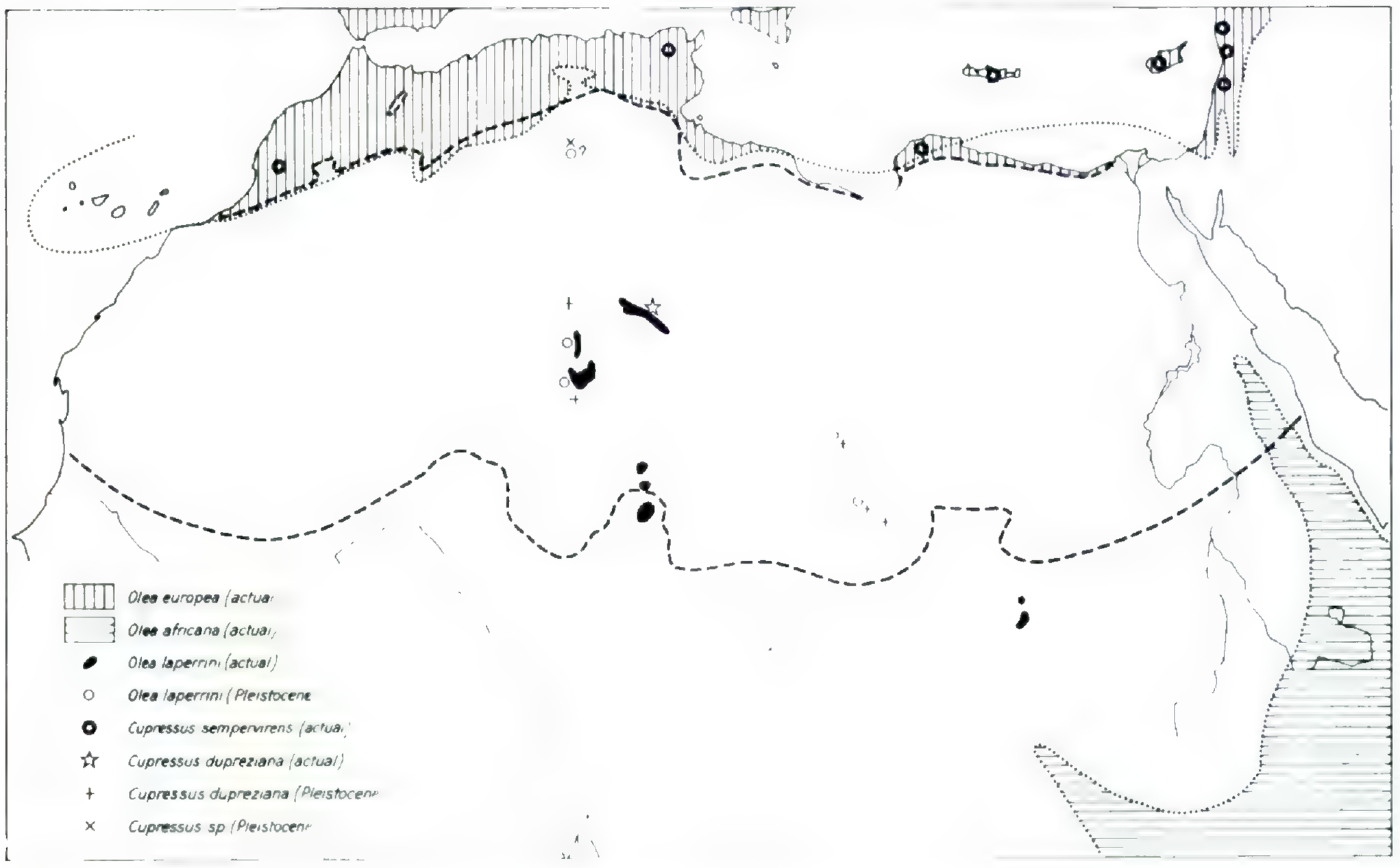

FIGURE 10. Distribution of Saharan mountain endemics compared with those of related species and known Pleistocene sites.

the genus *Anabasis* is represented by *A. aretioides* and *A. oropediorum* of the southern flank of the Saharan Atlas and *Suaeda* by *S. monodiana*, *S. ifniensis*, and *S. arguinensis* of oceanic Sahara. Also added can be *Pulicaria volkoskyana* of the southern Sahara and *Salvia chudeaui*, a vicariant of *S. santolinifolia* of the Sind, *Anvillea radiata*, *Gaillonia reboudiana*, and several representatives of the genus *Tamarix*, always a difficult group to interpret.

III.3.3.2—*Endemics of European Origin.*—Listed, because of lack of a better way, besides endemics of Mesogean origin, are some species whose affinities are debatable but whose affinities derive more from European and Eurasian taxa. The majority of them are localized on the summit of Tibesti where *Ephedra tilhoana*, *Artemisia tilhoana*, *Asplenium quezellii*, *Hyoscyamus tibesticus*, and *Galium uniflorum* appear as relatives of *E. distachya*, *A. alba*, *A. lepidum*, *H. albus*, and *G. spurium*. The case of *Helosciadium muratianum* and *Epilobium mirei* from the lakes of Borkou is comparable as these species are very close to *H. nodiflorum* and *E. parviflorum*. Finally *Erythrea minutissima* from Aozou in Tibesti, doubtlessly derives from *E. pulchella*, and in Hoggar *Potamogeton hoggariensis* from *P. pusillus*.

III.3.3.3—*Endemics of Tropical Origin.*—The endemics of tropical origin are less numerous in the Sahara than the endemics of Mediterranean origin despite the numerical dominance of the tropical element. In fact, with very rare exceptions the endemics of tropical origin occur only in special territories, especially in the mountains of the Sahara and coastal zones; the southern Saharan fringe likewise represents a very special case. As a result, the Sahara does not feature

endemics of tropical origin for 9/10 of its surface, with the exception, however, of *Crotalaria saharae*, and perhaps also *Lotononis dichotoma*. It is evident that this peculiarity traces to a recent, indeed extremely recent, origin from a floristic background of the Sahelian type in the Sahara.

I shall examine successively the endemics more or less associated with the Sahelian flora, those which belong to the "Rand Flora," and finally tropical endemism of the montane type.

Endemism of Sahelian Origin.—It is manifested fundamentally in the southern Sahara, even on the southern bases of the Hoggar and Tibesti massifs. Certain species are, from all evidence, recently evolved micromorphs, such as *Pegolettia dubieffiana* and *Bergia mairei* (Quézel, 1954) on the southern base of Hoggar derived from *P. senegalensis* and from *B. suffruticosa*. In the northern Sahara *Sporobolus tourneuxii* (southern Tunisia) and *S. lanuginellus* (southern Morocco) belong without a doubt to this group, as well as the rare *Crotalaria vialattei*.

On the other hand, although one often lacks scientific contributions to the exact division of these species, there truly seems to exist, on the mountain massifs of the southern Sahara, quite a collection of species which appear to be primarily limited to this zone, even if they penetrate locally in the Sahelian territory (notably on the northern mountain massifs Adrar of Mauritania, Air and Ennedi). Such appears to be the case for *Coelachyrum oligobrachiatum* and *C. brevifolium*, *Cenchrus montanus*, *Eleusine flagellifera*, several *Tribulus* (*T. alatus* and *T. ochroleuchus*), *Anticharis linearis*, *Blumea gariepina*, and on the Adrar of Mauritania for *Barleria schmittii*.

Endemism at the Level of the "Rand Flora."—A certain number of endemic species appear to be able to be referred to this source, which we have characterized precisely above. Such is the case for the endemics belonging to the genera *Caralluma* (*C. venenosum*, *C. sinaica*), *Mesembryanthemum* (*M. theurkhaufii*, *M. gausseni*), *Wahlenbergia* (*W. etbaica*, *W. tibestica*, *W. bernardi*), and also *Lotononis riouxii*.

It is likely that the elements generally considered to be of Macaronesian origin ought to be included here. This is the case for the cactoid euphorboids, and in particular for *Euphorbia balsamifera* and *E. regis-jubae*, as well as a certain number of species designated above as belonging to the Mediterranean flora (*Kalanchoe faustii*, *Commelina rupicola*) which extend more or less into the Saharan zone.

Endemism of the Montane Type.—I have already analyzed this on several occasions (Quézel, 1958, 1964a) and will here only recall the conclusions.

Montane Endemics of Indigenous Origin.—In this category is united a small group of species which represent vestiges of an indigenous predesert flora of the massifs. Such is the case for: *Pentzia monodiana*, *Ficus teloukat*, *Commicarpus montanus*, *Bidens minuta*, *Pluchea crenata*, *Tripogon multiforum*, as well as a group of vicariant endemics belonging to the genus *Rhynchosia* (*R. lynesii*, *R. tibestica* and *R. airica*).

Endemics of African Highland Origin.—These are taxa derived from lines still largely found on the tropical African mountains and the Ethiopian plateaus.

We can cite *Albuca septentrionalis*, *Chloris tibestica*, *Clematis tibestica*, *Trichodesma giganteum*, *Pentas tibestica*, and *Phagnalon tibesticum*, vicariants, respectively, and truly extremely closely related to *A. abyssinica*, *C. notocoma*, *C. simensis*, *P. carnea*, and *P. hypoleucum*.

Endemics of Montane-African Origin.—All localized on the summit of Tibesti, despite their rarity, they represent one of the most remarkable curiosities of the massif in a singular ecological environment, where *Erica arborea* also appears. The following can be cited: *Agrostis tibestica*, *Avenastrum tibesticum*, *Festuca tibestica*, *Silene mirei*, *Crassula tibestica*, *Helichrysum monodianum*, *Dichrocephala tibestica*, respectively related to *A. pilgeriana*, *A. lachnantha*, *F. abyssinica*, *S. macrosolen*, *C. pentandra*, *H. foetidum*, and *D. chrysanthemifolia* (Bruneau de Miré & Quézel, 1959). *Nepeta tibestica* is near several Ethiopian species.

Finally, on Tibesti exist rare endemics of Sudanese origin, localized particularly at the level of the fumaroles of Touside, at approximately 3,000 m altitude: *Oldenlandia toussidana* close to *O. goreensis* and *Fimbrystilis minutissima* vicariant of *F. oligostachys*.

IV.—Historical Interpretation of the Vegetative Population of Mediterranean and Saharan Africa

The present flora of Africa now situated to the north of the Sudano-Angolan floristic region is considered to be the result of paleoclimatological, paleoecological, and paleogeographical influences, persisting since approximately the beginning of the Tertiary, on the different vegetative assemblages which have evolved there but also on those which have been able to migrate there for various reasons.

The interpretation of these phenomena is extremely complex, and it would be ill-timed to try to give an analysis of it here, besides all is relative and subject to caution. However, a certain number of scientific papers, in general recent, have brought to these questions new precise details and actually permit one to comprehend, if not the totality of the phenomena, at least part of them.

These contributions have essentially treated the paleoclimatological and paleobotanical aspects.

IV.1—Contributions of Paleoclimatology and Paleobotany

We begin with a consideration of the Paleocene.

IV.1.1—*Paleocene*

If one looks at it somewhat diagrammatically and if one confines it essentially to the African continent, it seems likely that the regions studied here were affected in the Paleocene by a climate essentially of the equatorial type over the entire current Sahara (Millot, 1964; Greenway, 1970) and assigned by the latter to a "Tropical Rain Forest." The true Maghreb was related to a cooler climate, permitting the formation of a "Temperate Rain Forest." But Africa, a part of Gondwanaland, has not been reunited to Eurasia, as according to Dewey et al.

(1973) the connections between these two continents would not be prior to the middle Miocene.

From the point of view of the vegetation it appears that the Paleocene flora has not played an important role in the formation of the true Mediterranean Saharan stock, as is confirmed by the findings of Boureau (1958), and in palynology by those of Roche (1974), Jardine et al. (1974). Inversely, it is to this period that a large portion of the biogeographical affinities existing between the ancient and the new continent are affirmed, since America and Europe remained in contact at least to the middle Cretaceous.

If the flora corresponding to this period is well known in the Sahara, the same is not true for the region corresponding to the present Maghreb. The results obtained by Medus (1971) for the Mesogean Cretaceous flora remain in effect without significance for the later flora, the plant groups represented by *Classopolis* and *Normapolles* appearing to be end points.

On the other hand, it is very probable that the establishment of the very numerous taxa common between Europe and North America dates from this period in an area north of the Tethys (Raven, 1973).

The same is true for the meso-hygrophylic flora (*Acer*, *Aesculus*, *Cercis*, *Carpinus*, *Epimedium* incl. *Vancouveria*, *Fraxinus*, *Euonymus*, *Ostrya*, *Platanus*, *Populus*, *Quercus*, and also *Pinus* and *Juniperus* etc.) and the meso-xerophytic flora (*Arctostaphylos*, *Amelanchier*, *Arbutus*, *Berberis*, *Celtis*, *Helianthemum*, *Lavatera*, *Lycium*, *Rhamnus*, *Rhus*, *Salvia*, *Styrax*, *Smilax*, *Viburnum*) or also the xero-eremic flora (*Aristida*, *Boerhavia*, *Fagonia*, *Frankenia*, *Cleome*, *Evax*, *Talinum*, *Trianthema*, etc.).

The existence of a more or less xeric flora in Africa appears probable in this period, in particular in the southeastern part of southern Africa where Greenway identified a "subtropic woodland shrub" where, at least in part, the ancestors of the "Rand Flora" could have evolved. In contrast, because of the position of the equator, nothing like it appears to have existed in North Africa.

IV.1.2—*Oligo-Miocene*

The displacement of the equator toward the south permitted the formation in Africa of climates and types of vegetation closer to those presently observed, especially in the southern portion (Axelrod & Raven, 1978).

In the Oligo-Miocene present north tropical Africa was essentially occupied by a "temperate rain forest" in the area of the present Sahara, and by a "subtropical woodland savana" in the area of the present Mediterranean region, with a sclerophyllous "subtropical evergreen forest" on the mountains. According to Axelrod and Raven, this woodland savanna, by its floristic composition (Caesalpinieae, Mimoseae, Pittosporaceae, Combretaceae) seemed already characteristic of a climate with the presence of a dry period.

The sclerophyllous forest of North Africa with a dominance of *Quercus*, *Juniperus*, *Pinus*, *Laurus*, *Pistacia*, and *Olea* seems to have evolved in the Miocene and to have extended itself into the Pliocene.

Several important phenomena deserve emphasis in this period: in tropical

Africa there is the evolution of a montane flora in the region of the volcanic massifs which, incidentally, have allowed some notable floristic and faunistic exchanges (Hedberg, 1965) between northen Africa and the tropical south since the Miocene. Similarly, the appearance of considerable relief should have multiplied biotypes favorable to the expansion of a xerophytic flora (especially the "Rand Flora") of tropical origin.

Finally, more to the north, the existence of arid phases in what is presently the Maghreb, associated with the building of mountain chains elevated on the site of the Tethys, constituted a millieu eminently favorable to the speciation and migration, especially from the east to west, of the floras (Stebbins, 1974).

IV.1.3—*Pliocene*

If the existence of phases of aridity and in particular the appearance of at least a local or temporary dry season was already recognizable in the Miocene in northern Africa, it was in the Pliocene that this worsening of the climate was accentuated. The appearance of the first eolian deposits in the Sahara (Butzer & Hansen, 1968), date from the beginning of the Pliocene, and Coppens & Koeniguer (1976) indicate that in the Koro-Toro region *Tamarix* and *Retam* forests were part of a prehistoric stratum dated 4–5 million years. Maley (1977) provides several paleontological and geomorphological arguments for this interpretation and thinks that it is in this period that the desert climate started to establish itself in northern Africa, paralleling a perceptible lowering of the temperature in the Mediterranean region (de Lumley, 1976).

The palynological analyses carried out at Hoggar by Van Campo et al. (1965), and then at Kourkour in Egypt (Van Campo et al., 1968) on sediments dating from the end of the Pliocene, demonstrate, without entering into the fine points of the discussion, a flora ultimately rather closely resembling the present flora, and one in which elements called Saharan and tropical predominate; the presence of pollen belonging to northern taxa appears more related to long distance transport. In Saoura (Van Campo, 1973) the results were comparable for the most part.

It seems, therefore, that from the Pliocene, and with an influence more or less great throughout this period, a desert climate established itself in the major part of the Sahara, at least in the lower altitudinal zones. Thus desertification began at least 5–6 million years ago and certainly increased up to the first pluvial phases of the Pleistocene, in direct correlation with the advent of the glaciations.

In Mediterranean Africa, on the contrary, paleobotanical contributions demonstrate a very diversified flora in the Villafranchian in which occurred, besides tropical elements or Macaronesian elements presently absent, not only the major portions of the contemporary climax forest but also some of the more hygrophylic elements now characteristic of the Euxino-Hyrcanian zone (*Juglans*, *Pterocarya*, *Fagus*, *Ulmus scabra*, *Carpinus*) indicating a climate certainly more humid and warmer than the present climate; but the existence of a dry summer

period was locally also probable, as was confirmed by the presence of *Olea*, *Quercus suber*, and *Q. ilex*.

IV.1.4—*Pleistocene*

Without entering anew into detail, the appearance of glacial periods, with which the pluvial phases of Africa were more or less directly (Maley, 1976) associated, have created considerable confusion concerning the relationships of the floras of Mediterranean Africa and the Sahara.

In Mediterranean Africa the existence of drier phases and of more variable climates eliminated a certain number of elements, particularly the major segment of present Hyrcano-Euxinian or Macaronesian types. The cold phases and the establishment of glaciers on the high mountains permitted the establishment (despite the persistence of the Strait of Gibraltar) of a certain number of circumboreal elements. Finally, the extension of the steppes, especially *Artemisia* and Chenopodiaceae, appeared to be a phenomenon generally associated with the increase of continental climates begun at the end of the cataglacial phases. If several glacial periods of variable nature followed upon each other in North Africa, it appears very probable that the last one was the most intense, as the study of the flora and especially of the residual or relic floras clearly shows.

In the Sahara, the impact of pluvial phases on the flora and the vegetation in the Pleistocene has been considerable (Rognon, 1976). Just as we have shown for the last one on fossil guano of *Procavia*, which it is impossible to impute to wind dispersal (Pons & Quézel, 1956, 1957; Quézel & Martinez, 1958, 1961), the increase in precipitation wiped out a great part of the desert and permitted the exchange of species between the Mediterranean and tropical regions. This phenomenon, cyclic during the Pleistocene, affected profound changes in the pattern of the floristic domains and in the migrations of the flora, the interpretation of which has not always been clear; I shall return to this question later.

IV.2—PROBLEMS RELATIVE TO THE ESTABLISHMENT OF THE PRESENT FLORAS (Fig. 11)

For greater ease I shall examine these problems successively in terms of the biogeographical origin of the different elements.

IV.2.1—*Mesogean Elements*

I am uniting under this term at the same time Mediterranean, Irano-Turanian, and Saharo-Arabian taxa. All these conform to climatic criteria, among which the presence of an essentially summer dryness (sometimes replaced by a nearly constant dryness for the Saharan taxa) is the major characteristic; the distinction between the Mediterranean and Irano-Turanian elements is especially of geographical origin since the thermal criteria (Daget, 1977; Nahal, 1976) are not determinants.

If the existence of a period of annual dryness is probable (we have seen that

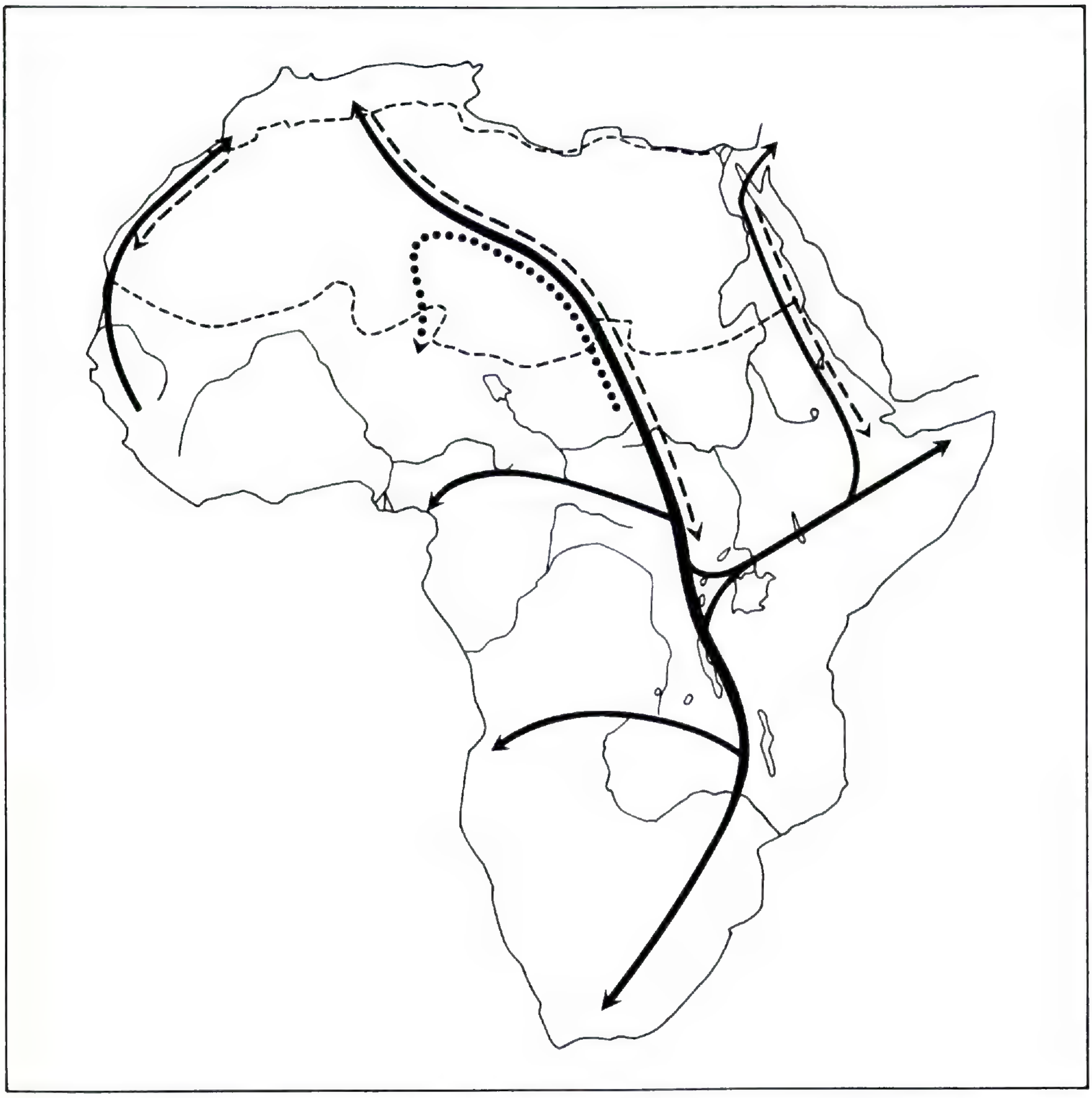

FIGURE 11. Migration routes in Africa (Pliocene and Pleistocene). Heavy dark arrow: tropical elements; dotted arrow: Southern Saharan orophilic elements; dashed arrow: Mediterranean elements.

it has existed since the Pleistocene), it is not obvious that a precipitation regime of the Mediterranean type (Axelrod, 1973) existed at this period. It would most certainly have appeared in the Pleistocene, connected with the initiation of the glacial phases. According to Axelrod, this climate would have been only periodic during this period.

The contributions relating to the perturbations caused by the glaciations on the Mediterranean flora are beginning to be well known, and have revealed themselves to be very remarkable.

Under these conditions, the Mesogean floristic assemblage has since its inception, undergone incessant onslaughts, especially climatic, which render global interpretation difficult but which have in every way greatly favored speciation.

IV.2.1.1—*Sources of the Mesogean Flora.*—Sources of the Mesogean flora are many, both Eurasian (indeed Laurasian) and African.

The Eurasian elements, whose arrival in Africa did not appear to be prior to the disappearance of the Tethys at the Neogene, are composed of numerous types common to Europe and North America (Raven, 1973), but also often to north-tropical Asia (Meusel, 1971), doubtlessly dating from the Cretaceous; at least their common ancestors had evolved before the separation of these two continents. Here are found at one and the same time elements of the temperate forests designated above, a great deal of which is still present in North Africa, but also elements which are clearly more xeric (particularly *Salvia*, *Lavatera*, *Berberis*, *Smilax*, *Arbutus*, *Rhamnus*, and various Cistaceae). These two floristic types had certainly been present in North Africa during the second part of the Tertiary, and the first was in part eliminated at the time of the climatic modification connected with the beginning of the glaciations. The Euxyno-Hyrcanian and Macaronesian elements had by then been extremely reduced and only traces of it have persisted. On the Constantino-Tunisian coast, always very humid, can be noted *Chrysosplenium dubium*, *Epimedium perralderianum*, *Quercus afares*, and on the Moroccan oceanic coast (at least for the true Macaronesian taxa of indisputable Mesogean origin) *Asparagus*, *Chenolea*, *Helianthemum*, *Hypericum*, *Rhus*, *Lithospermum*, *Andryala*, (and indeed Laurasian), *Drusa*, and *Cneorum*.

This flora, Eurasian in origin and certainly evolved on the northern side of the Tethys, has become widespread over the whole of the true Mediterranean region, but also more to the east even to oriental Asia. The xeric types whose appearance doubtlessly goes back to the more or less cyclic dry periods, which date from the middle of the Miocene (Andreànszky, 1963; Demangeon, 1958) and which have been substantiated by a certain number of macro or fossil pollen (Pons, 1964), have profited in addition from the elevation of the Mesogean mountain massifs. It is certainly from this period that the establishment of orophilic taxa extending from the Atlantic to the Himalayas must be dated; the greater part of these have given birth to endemic vicariate series. Examples of this are genera like *Cedrus*, *Abies*, and *Berberis*, the arborescent *Juniperus* of the Mediterranean, as well as the major part of the elements actually considered as oro-Mediterranean (Quézel, 1957).

These elements have contributed a great deal to the evolution of the Mediterranean flora, especially the sclerophyllous forest, since the Pliocene where, according to Axelrod & Raven (1978), it occupied a large part of the Maghreb and the northern Sahara and reached the mountain massifs of the central Sahara. The elements of tropical origin (cf. below) were largely associated with it. It appears, however, that from the middle Pliocene there may have developed a state of aridity on the southern margins that leads me to agree with the results cited below for Koro-Toro (Coppens & Koeniguer, 1976).

During the Pleistocene, and certainly during several reprieves, the alternation of the truly arid desert phases with wetter phases in the whole of the true Sahara has affected interesting migrations of the floras. The example of the last pluvial

phase can give us a good idea of this (Quézel & Martinez, 1961). Under these conditions Mediterranean taxa could have survived in certain localities, particularly on the Saharan mountains, side by side with other elements of African origin. The existence of several such fluctuations is the reason why a certain level of endemism is evident in this flora. The most remarkable example is that of *Cupressus dupreziana*, at least for the strains of Mesogean origin. On the contrary, as we have indicated (Bruneau de Miré & Quézel, 1961) *Olea laperrini* and *Myrtus nivellei* belong to the montane African strains.

IV.2.1.2—*The True Saharo-Arabian Flora.*—The flora truly considered to be Saharo-Arabian and therefore of northern origin, could only have evolved following the establishment of dry phases forming true deserts. It does not seem possible, as I discussed earlier, to place the start of this phenomen in North Africa before the Pliocene, but its extension into the Sahara was certainly concomitant with the glacial phases, especially the appearance of interpluvial phases, of which the present one appears to be the most intense (Quézel, 1958). The Saharo-Arabian taxa belonging to the Mesogean flora are numerous. This is the situation particularly for those that belong to the Crucifereae, Caryophyllaceae, Resedaceae, Boraginaceae, Leguminosae (p.p.), Tamaricaceae, and Umbelliferae but also to the Zygophyllaceae, and to a part of the Leguminosae, as well as the Gramineae. The existence of a certain number of taxa common to the African desert and the American desert: *Fagonia*, *Zygophyllum*, *Frankenia*, *Oligomeris* (Raven, 1973), likewise points in favor of a more precocious differentiation of certain taxa. It is always difficult to set a limit between the Saharo-Arabian elements and those which belong for the most part to the "Rand Flora," and whose origin is African (cf. below). Endemism is quite important in this flora and the relative antiquity of its establishment in the Sahara is confirmed.

IV.2.1.3—*The Irano-Turanian Flora.*—This flora enjoys only a minor role in North Africa. It characterizes the steppes and continental deserts with hot summers and very cold winters, climatic characteristics very close to those proposed by Adam (1969) to characterize the end of the glacial phases of the Quaternary. It is in fact very probable that this type of climate has been able to persist elsewhere on mountain massifs, even during the course of the interglacial periods, and which has conditioned the appearance of this flora from preexisting taxa, especially the Salsolaceae, Leguminosae (*Astragalus*), and Compositae (*Artemisia*). The Ephedraceae have also benefitted much from this type of climate.

If it is presently in eastern and central Asia that the Irano-Turanian flora reaches its optimal development, it is appropriate to remember that in the present Mediterranean region the retreat of the glaciers has, in a way, brought about an almost constant expansion of a pollen flora of this type during several thousand years, based particularly on Salsolaceae, Ephedraceae and *Artemisia* (Reille, 1975; de Beaulieu, 1977), which also appeared on the Atlas Mountains (Reille, 1976) and which is difficult not to associate with a climatic type of the present Irano-Turanian type. Some quite similar climatic conditions persist in North Africa on the high mountains and plateaus, which have likewise permitted, even

to our day, the maintenance of a certain number of its representatives. Endemism has been much reduced here, and this testifies to the recent development of this flora, whose different elements could nevertheless have persisted since the initiation of the glacial phases on the high mountains (Atlas Mountains), where several endemics (*Artemisia*, spiny *Astragalus*) have evolved.

IV.2.1.4—*African Elements in the Mesogean Flora.*—The Mediterranean flora of North Africa appears at first glance to have only remote connections with the flora of African origin which, however, had occupied these territories in the Paleogene, and even during a part of the Neogene. In fact, a closer examination shows that this interpretation deserves to be modified slightly.

In effect, if one makes an exception of the recent immigrants cited above—these doubtlessly participating accidentally, especially in the case of hygrophilous or anthropophilous species—it is possible to associate a certain number of groups of species now present in North Africa with the African flora.

The first is that of species present at the same time in the savannas of Africa, certain mountains of the Sahara, and the Mediterranean region (at least in part). This is the case particularly for the Gramineae, especially the Andropogoneae noted earlier, which as a group have not changed from a taxonomic view over their entire area of distribution. For this reason I do not think that their occurrence in the Mediterranean region or in the Sahara is ancient; this certainly happened during the Quaternary pluvial phases, which permitted an intermeshing of Mediterranean and tropical assemblages in different spots. These exchanges have been brought about on several occasions during the course of the Pleistocene, but the thermal demands, relatively large for these species, permitted them to become established and to persist in the Mediterranean region, where they are, however, confined to the warmest zones (Thermo-Mediterranean Stage; Ozenda, 1975; Quézel, 1976). On the contrary, the Sahelian species characteristic of the "Desert Savanna," e.g., *Acacia panicum* (Maire, 1940; Quézel, 1965) from all evidence penetrated into the Sahara only at the end of the last pluvial stage (doubtlessly after several other phases of extension) but did not reach the Mediterranean regions because of their thermal demands.

A second interpretation is precisely that of the "Rand Flora." This ancient eremic African flora, perhaps earlier than the Oligocene, is difficult to assess, especially because of the exchanges which could have occurred across Africa, notably in the Pliocene, with the Saharo-Arabian flora. We have already supplied a possible list above, but it is necessary to recall that a part of the true Macaronesian flora could have been related to it, especially the crassulescent or succulent elements (Fig. 7).

In fact, a large number of Saharan genera have a north-south tropical distribution in Africa, and it is possible that new research will again expand this list. Here may be noted again the genus *Pituranthos* which has 2 species in Namaqualand, as well as *Zygophyllum*, *Mesembryanthemum*, *Tribulus*, *Cleome*, and *Suaeda*.

The presence in the American desert of elements usually connected to this flora should be noted and certainly verifies the antiquity of its establishment.

Examples are *Oligomeris*, *Talinum*, *Trianthema*, and also perhaps *Fagonia*, *Boerhavia*, and *Cleome*.

A third group is made up of species whose present distribution is indisputably Mediterranean, but which belong to essentially tropical genera. Raven (1973) believes and emphasizes, rightly so, that these taxa are not extant in America, and that their evolution and the migration into the Mediterranean region must therefore have taken place after the separation of these continents. It would not have been prior to the Miocene. It also is highly probable that a certain number of representatives of the vegetation of African origin which had developed before the effacement of the Tethys, particularly in North Africa, could have lived there or formed types adapted to the new climatic conditions. Such seems particularly to be the case for the genera *Olea*, *Ceratonia*, *Tetraclinis*, *Chamaerops*, *Laurus*, *Myrtus*, *Ficus*, *Maytenus*, and *Capparis*.

In fact, there was also the possibility of exchange between the Cape and Mediterranean regions. Burtt (1971) supplies several examples of this, and even if certain ones can be interpreted as anthropozoogenic, it is clear that the present distribution of the genera *Erica* (Fig. 8), *Lotononis*, *Helichrysum*, and *Pentzia*, as well as the section *Hastati* of the genus *Rumex* (Meusel, 1971) cannot be interpreted differently. The existence of genera from all evidence vicariants again confirms this, together with the antiquity of the separation. This is the case for the genera *Echium*, *Thymelaea*, *Iris*, *Mercurialis*, and *Buxus*, represented in South Africa by the genera *Echiostachys*, *Passerina*, *Moraea*, *Seidelia*, and *Notobuxus*. Among the Fumariaceae the affinities between the genera *Rupicapnos* and *Trigonocapnos*, *Platycapnos* and *Discocapnos*, *Sarcocapnos* and *Cysticapnos* should be noted.

IV.2.2—*Northern Elements*

I include in this term the floristic elements of European, Eurasian paleotemperate, or circumboreal origin.

In fact, it appears that originally the majority of these were not separate from certain constituents of the true Mesogean flora, and I have discussed this previously. It is evident that the climatic fluctuations experienced since the Pliocene have greatly modified the representation of species belonging to this biogeographical type. The dry Pliocene phases in part weakened it, and the same thing happened during the glacial periods, at least for the types most sensitive to cold and dryness. On the other hand, the glaciations in North Africa permitted the appearance of a number of circumboreal or new alpine elements, especially on the Atlas Mountains, via the Iberian Peninsula (Quézel, 1957). A migration by the Sicilian-Tunisian bridge was equally possible and would explain the presence in the northeastern Maghreb of a certain number of taxa of European origin.

Several lineages which are doubtlessly related to these elements have even reached the mountains of the Tibesti, but here it is a question of hygrophilic or indeed clearly heliophilic species or truly xerophilic species (cf. above). In my opinion their appearance on this massif could not have been prior to the Pleistocene, at least based on our present state of knowledge.

IV.2.3—*Tropical Elements*

Autochthonous in North Africa and in the Sahara after the Paleocene, indeed after the Cretaceous, they have been progressively eliminated from them by the climatic transformations which came about after the end of the Miocene, as well as by the glacial episodes of the Pleistocene which assured the quasi-defintive destruction of them. In fact, as mentioned above, the tropical elements still play an obvious role in the flora known as "Mesogean" and I will not return to this matter.

It is still necessary to consider here the question of the survival, essentially on the Saharan mountains, but also on the maritime fringes of the Sahara—indeed of Mediterranean Morocco—of an important group of tropical elements, for the most part with montane affinities, which pose the problem of the persistence "in situ" of certain elements belonging to this biogeographical type.

The Moroccan Coast.—It has already been discussed with respect to the Macaronesian element and a part of this element is very near, if not the same, as the "Rand Flora." However, this position should not be generalized; some Moroccan endemics of tropical origin are probably better considered to be differentiated vestiges, "in situ" doubtlessly since the Pleistocene. The most remarkable case is certainly that of *Acacia gummifera*, sole representative of the genus adapted to the Mediterranean climate. *Andrachne* and *Commelina rupicola* could also be cited.

The Red Sea Coast.—I have already discussed this and it will suffice to stress the presence here of an appreciable number of taxa of African montane affinity, but which do not appear to be cases of endemism. This phenomenon is without doubt connected with the fact that these populations are always in contact, through the Sudanese coastal mountain chains, particularly the Erkowit Mountains, with the flora of the Ethiopian plateaus. One can also envision a recent establishment, which is in fact in contradiction with the paleoclimatic data.

The Mountains of the Central Middle Sahara.—The thorough exploration of Hoggar (Maire, 1940; Quézel, 1954), of Tibesti (Maire & Monod, 1950; Quézel, 1954), of Air (Bruneau de Miré & Gillet, 1956), of Ennedi (Carvalho & Gillet, 1960), of Jebel Gourgeil (Quézel, 1969), of Jebel Marra (Wickens, 1977), has brought to light a whole flora of African origin which appears to represent well the traces of the flora which colonized these massifs before the appearance of the severe desert formations which characterize the southern Sahara today.

If this flora is still incompletely known, and certain taxonomic revisions appear desirable, it is nevertheless possible to discern there at least their groups: a montane African group, an autochthonous montane group, and a group of oro-African origin.

I shall not review here the list of species which are associated with them, the affinities which may relate certain taxa to the "Rand Flora." I shall note, however, that *Tibestina lanuginosa*, described by Maire as endemic to Tibesti, corresponds in fact (Scholz, 1966) to *Dicoma capensis* of southern Africa and *Eleocharis tibestica* (Quézel, 1959) to *E. intricata* of Madagascar and southern Africa.

On the other hand, from the point of view of categorizing taxa, it appears possible to associate the first two of these groups, more or less directly to the "montane rain forest" (sensu Greenway, 1970), whose appearance on the mountains of the Sahara, can be traced back to the Paleocene; according to Greenway, however, its extension on the other African massifs dates more from the Miocene.

Although that is possible, one cannot pin down the position of this flora to this period; migrations have actually been possible during the pluvial phases of the Pleistocene, a period which really appears to correspond with the differentiation and development of the oro-African flora.

In fact, one can question whether the montane axes of Africa (cf. Fig. 11) have not constituted a route of temporary migration for the various African floras. The results published by Sah (1967) for pollen derived from the region of Lake Kivu and doubtlessly dating from the end of the Pliocene seems to confirm this, since many tropical families still present in part on the Jebel Marra, and indeed Tibesti, appear there, as well as families with more temperate affinities (Cruciferae, Buxaceae, Ericaceae, Geraniaceae). It is certainly via this route that the majority of exchanges between the African highland flora—and indeed the Cape flora—and the flora of the present Mediterranean region have been brought about. The "Rand Flora," as well as the present Macaronesian flora to which it is related, without a doubt benefitted equally from this migration route, which finally was only closed periodically during the Pleistocene especially during the interpluvial phases.

V. Conclusions

This analysis of the Mediterranean and Saharan flora permits me to draw a certain number of conclusions, particularly if one attempts at the same time to interpret the origin of the phytogeographic elements that exist there.

I have stressed above the principal differences which can be observed between the Mediterranean and the Saharan floras in terms of representation and number of genera, percentage of endemics, or as a function of the present distribution of geographical types; I will not return to this.

It is, on the other hand, interesting to emphasize that the general effect of the flora points to a relatively recent origin since the original stocks did not differentiate, primarily "in situ" but well to the south of the northern side of the Tethys. The appearance of the Mesogean flora in Africa seems, on the whole, to have been contemporary with the upper Miocene.

From the viewpoint of climate, the replacement of a climate of a truly equatorial or tropical type by a more variable regime having dry periods seems to date essentially from the Pliocene, at least in the true Saharan region; more to the north, relatively dry periods appear to have already existed in the Miocene.

In fact, it is becoming clearer that the Mesogean flora ought to be considered as a flora of discrete additions provided at the same time from Eurasian and tropical elements, which evolved in and migrated from very distinct climatical and geomorphological environments, and which have been disclosed as being emi-

nently favorable in every way to the phenomenon of speciation. It is probable that the climatic instability already evident in the Miocene and especially in the Pliocene, and exacerbated during the Pleistocene, has been a determining factor in the appearance of numerous species. This phenomenon has again been favored by orogenic phases which followed upon each other during the second part of the Tertiary in this entire region.

On the contrary, the differentiation of the Mediterranean, Saharan, and Irano-Turanian bioclimatic entities seems to be directly associated with great climatic fluctuations in the Pleistocene which finally, and doubtlessly with several lulls, redistributed in the area a relatively homogenous floristic base, at least as to its origin.

The tropical element, a part of which has participated in the formation of the floristic base of the Mesogean since its inception, has always been largely eliminated from Mediterranean Africa for essentially climatic reasons; these have always partly continued to exist in the Macaronesian zone, even though they have been decimated by the desertification of the mountains in the present southern Sahara. Certain elements, especially adapted elements such as the Sahelian flora and the eremic African flora, have continued to enjoy an appreciable role in portions of the Sahara that continue to benefit periodically from rains of the tropical front.

All these conditions have been favorable, theoretically at least, to the development of a rich and diversified flora; the number of endemics of the African Mediterranean zone (a little less than 30%) really shows this. In the Sahara the climatic rigor and also an excessive climatic instability during the Pleistocene have limited this phenomenon (about 12%). It is also certain that it is the therophytes which have most broadly benefitted from this climatic context, since they represent about 50% of the Mediterranean flora in North Africa and also of the Saharan flora. These high percentages have only been surpassed by those which appear in the area of the northern Sahelian flora where they reach almost 70% (Quézel, unpublished). It is, moreover, among the therophytes that endemism is equally high. This phenomenon is above all evident in the typically Mediterranean families: Caryophyllaceae (nearly 60% of the annual species are endemic), Cruciferae (more than 70% of the species and 11 genera are endemic), Resedaceae, Umbelliferae, and Scrophulariaceae.

It is also interesting to note in the matter of endemics that in the Mediterranean region, North Africa has especially benefitted from the functioning of the Ibero-Mauritanian zone, or better, Ibero-Moroccan, through which more than 500 of the endemic species presently recorded in North Africa were formed. This figure is doubled if one adds to these the Ibero-Mauritanian species. On the other hand, west-central Algeria and Tunisia have only a very intermediate percentage of endemism, at least at the circum-Mediterranean level; the case of Cyrenia is not very different, although this region has profitted more from endemics of Mideastern origin.

In the Sahara, apart from the endemics of the northwestern Sahara which reveal at least in part an Ibero-Moroccan influence, and some highly residual species, the endemic species are generally much more widely distributed, doubt-

lessly because of the climatic and geomorphological homogeneity (at least in the northern part of the Sahara for the latter). Besides endemism, and perhaps more remarkable, is the existence here of residual and biogeographically very diversified floras. This phenomenon, although largely masked today by extreme aridity little compatible with the development of plant life, reflects in fact the constant climatic disturbances that have assailed this region since the end of the Tertiary and which, with several lulls, have been able to modify the plant life totally.

In place of the idea of a "Saharan barrier," a myth which has persisted tenaciously in the thinking of a great number of phytogeographers up to recent times, it is appropriate to substitute the idea of a space periodically and transitorially desert. This Sahara, in the Neogene and at different times in the Pleistocene, has, locally at least, functioned as a favored place of exchanges between the African and Mesogean floras. But it still remains at the present time, and in spite of a climate particularly unfavorable throughout its entirety, a veritable conservatory for certain taxa which have followed each other since the end of the Miocene.

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COMPOSITION, ORIGIN, AND AFFINITIES OF THE MADAGASCAN VASCULAR FLORA

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ABSTRACT

The Madagascan vascular flora which is composed of over 160 families is exceptionally interesting not only because it is prodigiously rich and diversified, but because it has preserved a number of relicts. In this review, presented roughly according to the phylogenetic system of Cronquist, every family has been tentatively, although shortly, analyzed wih regard to its composition, origin, and affinity. The hypothesis that the Madagascan flora was a part of the large Cretaceous Gondwanian flora at the time when Angiosperms originated and that the flora became greatly impoverished on the African continent due to far-reaching climatic changes accounts for many present characteristics of the Madagascan flora. In this context the existence of a Madagascan region sensu lato (Madagascar, Mascarene Islands, eastern and southern Africa), where many austral genera or taxa of higher taxonomic rank exist—some of which belong to Magnoliidae and to the most primitive parts of Dilleniidae and Rosidae—becomes understandable. Equally understandable become many discontinuities of range and the existence of many endemic uni- or paucispecific genera. Briefly, the present Madagascan vascular flora probably resulted from a progressive differentiation of the autochthonous Gondwanian stock and natural introduction of taxa in time through long-distance dispersal.

In this paper, I do not intend, of course, to present an exhaustive enquiry concerning the origins and affinities of the Madagascan flora. I think an enormous amount of basic research remains to be done in order to get an accurate general view on the matter. And how could we do so, since we mostly cannot establish a satisfactory connection between taxonomic classification and distributional patterns, in order to express the true taxogenesis?

Since Perrier de la Bâthie and Humbert's geographical works on the Madagascan flora many papers and books have been published, but no new concept significant enough to have important implications has been proposed. Some recent publications of great interest pertaining to this matter have appeared, but they are not especially devoted to Madagascar. A very limited number of valuable papers have to be mentioned, insofar as they contribute to Madagascan phytogeography, such as those by Stearn (1971), Dejardin et al. (1973), Koechlin et al. (1974), Wild (1975).

In fact, any attempt at a comprehensive synthesis of this kind at this time would be premature because we need to know much more with respect to palaeobotany and phylogeny.

Although no important general conclusion has been reached concerning the biogeography of the Madagascan plants for some decades, the same does not hold true for strictly taxonomic knowledge, which has much progressed, thanks in particular to outstanding research by the late forester and botanist R. Capuron. We are indebted to him for an exceptional improvement in the analysis of the woody plants of Madagascar. But even in taxonomy we are far from having

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ANN. MISSOURI BOT. GARD. 65: 535–589. 1978.

0026-6493/78/0535–0589/$05.65/0

sufficient information, and, in spite of the efforts by Capuron and many others, among them the botanists of the Muséum National d'Histoire Naturelle and O.R.S.T.O.M., many families, certain of which are the largest such as the Poaceae, Orchidaceae, Euphorbiaceae, and Leguminosae, have not yet been revised in their entirety.

In 1959 Humbert posed a problem, which was in his opinion a very perplexing challenge to botanists and zoologists, namely, where and what have Madagascan taxa originated from? Have they as a whole been derived from a Cretaceous stock in place for a long time or are they for the most part newcomers that arrived there during the Tertiary and later. If the latter is the case, which seems supported by some evidence, how did seed plants manage to reach Madagascar from Australia or America or, in particular, from Africa with which so many links are evident? As viewed by Humbert, who principally limited his considerations to relations with Africa, plants might have reached Madagascar either by direct land migration (land bridges) or long-distance dispersal (by means of sea and wind currents, birds, bats, drift wood, rafts, etc.). In his paper, Humbert, far from discarding long-distance dispersal, discussed at length two aspects of the question; but in his opinion it was a secondary process that was not very effective. One can explain the immigration by sea water of a few plants in this manner, but these are well-known species which always remain confined to, or next to, sandy and rocky beaches. In particular, Humbert believed that long-distance dispersal could not explain the presence in Madagascar of certain genera such as *Cycas*, *Nepenthes*, and *Ceriops*. In the same way, although attaching more importance to wind currents, he did not trust in their efficiency. In order to support his thesis, he invoked evidence drawn from the Compositae. Let us take, he wrote, the three genera *Helichrysum* (100 species in Madagascar), *Vernonia* (100 species) and *Senecio* (60 species) which have a percentage of endemism close to 100%. In comparison with what we know about the evolution of Tertiary floras in the Mediterranean basin and East Africa, we must admit a similar differentiation in Madagascar. Any addition to the flora by long-distance dispersal would have diminished the percentage of endemism, which is in contradiction with known data. It is clear that in Humbert's opinion, we have to view the increasing number of species as the result of a differentiation from the ancestral flora, even though the relevant plants are readily dispersed.

I think Humbert's concept does not fully account for many fundamental problems with which we have to deal. Perrier de la Bâthie (1948), in contrast, suggested that differentiation might, at least for a small part, have proceeded from chance immigration, and he referred, in particular, to the case of *Calophyllum*, several species of which have differentiated in the Mascarenes and the Madagascan interior, from possibly only a single widespread species, namely *Calophyllum inophyllum*.

One could allege that many of the widespread species that we know, such as many littoral ones, are generally isolated and rather stable, although polymorphic, in every country where they occur. But this objection is hardly defensible for at least three reasons. First, every pioneer species is not necessarily

the potential source of a new "taxogenesis." Second, the pioneer species we know have not possibly had time enough to differentiate. Third, opportunities in relation with changes of environment may have not occurred.

However that may be with respect to present conditions, it is now generally admitted that past events dealing with biogeography have to be explained by the theory of plate tectonics. According to this, the history of the earth is a continuous process, and continents may be rafted as much as 2,000–3,000 km apart after having been joined, or, on the contrary, to become joined after a long separation. So, there is no longer any essential difference between long-distance dispersal and direct migration by land bridges. One can consider both of these mechanisms as the two extreme limits of a single process. The different biota of the Globe are presently massive wholes which have been built up slowly during geological times as plates approached to, or moved away from each other. Let us not forget that the opening of the South Atlantic began only 125–130 m.y. BP in the Lower Cretaceous. By the Paleocene, the gap between South America and Africa was only 800 km and "populated with volcanic islands" (Raven & Axelrod, 1974). Madagascar separated from Africa about the mid-Cretaceous and from India at the same time or possibly later, but opportunities for exchanges with Africa across the Mozambique sea barrier lasted a long time and are still presently possible. By mid-Cretaceous time, direct migrations between India-Madagascar-Africa and Australia became more and more difficult as these lands moved away.

If no essential distinction is made between the notion of long-distance dispersal and that of direct migration, then we have much more flexible bases at our disposal for attempting to understand biogeographical facts.

In Humbert's paper (1959), "Origines présumées et affinités de la flore de Madagascar" all the Madagascan flowering plants are briefly reviewed in turn. My present contribution is only a complement aimed to bring the Humbert compilation up to date, not only, of course, in taking new taxonomic and floristic data into account, but also in considering them in the light of the plate tectonic theory, which is now reliable enough to be taken as a foundation of biogeography. Further, certain families are emphasized either for distributional patterns that are especially significant in relation to Madagascan biogeography or for having been recently revised. Thus, such families or orders as Winteraceae, Canellaceae, Saxifragales, Theales, Tiliales, Malvales, Guttiferae, Celastraceae, Malpighiaceae, Meliaceae, Combretaceae, Araliaceae, Verbenaceae, Asteraceae, and others are worth detailed analysis.

With regard to relationships between neotropical and African-Madagascan floras, authors often concur in the belief that the species of the same genus or the members of the same species occurring on both sides of the Atlantic Ocean have not crossed the present ocean, but have always inhabited the site where they grow today. So, for 90 m.y. BP some genera or species would not have evolved at all. In my opinion, one should not forget that by the Lower Eocene (about 50–55 m.y. BP) the Atlantic probably did not yet form an absolute barrier for living beings. Dejardin et al. (1973) admitted judiciously, among other possibilities, that such a species as *Rhipsalis baccifera* could have reached Africa

a long time after the original separation of the continents. I agree with Raven & Axelrod (1974) that one must suppose that "numerous islands afforded ready migration across the opening Atlantic into the Early Tertiary." Later, difficulties for crossing became stronger and stronger but transmigration continued to occur. Although this process appears unlikely, just as evolution itself, yet so must it have happened.

In terms of the above explanation, *Christiana africana* is possibly a newcomer in either Africa-Madagascar or America, and the distributional patterns of families mentioned by Dejardin et al. (1973) such as Bromeliaceae, Rapateaceae, Humiriaceae, and Vochysiaceae, insofar as they can be comparable must also belong to the same explanation—and this even though several species of *Rhipsalis*, manifestly directly derived from the same ancestor, are in existence in Madagascar.

I think that the obstacle in the way of understanding biogeographical facts is presently not so much what has happened with oceans and sea barriers or geological considerations, but our own ignorance about plant taxonomy and phylogenetics. Statistical figures about composition and endemism percentages classically used since Perrier de la Bâthie (1936) and Humbert's (1959) works are interesting data, as also are the data provided recently by Dejardin et al. (1973), among others, but we now need multidisciplinary and biological monographs—why not by international teams?—of only a few especially chosen families.

Taking into consideration a number of recent important biogeographical works on the one hand, and, on the other, certain data from my own research, I am led to some general hypothetical principles which can be outlined as follows:

1. Primitive angiosperms originated in Gondwanaland (possibly in West Gondwanaland, according to Raven & Axelrod, 1974, with whom I agree), then extended their range northward long before Gondwanaland broke up, possibly during the last part of the Lower Cretaceous.

2. As soon as the Upper Cretaceous, two large floras must have been established: a Laurasian one (Magnoliaceae, Ranuculaceae, Amentifereae, . . .) and a Gondwanian one (Annonaceae, Winteraceae, Myristicaceae). The concept that the angiosperms empire is divided into two great floras, was recently, and rightfully I think, emphasized by Aubréville (1974a).

3. At the close of the Cretaceous and by the Early Palaeocene almost all modern families were in existence.

Every modern family has evolved sufficiently for adapting to new geologic or climatic conditions. Some have diversified in many directions, and they have succeeded in colonizing the most diverse regions on the Globe (Orchidaceae, Compositae, Poaceae, . . .). Others, even though narrowly specialized, have kept a combination of both advanced or very advanced characters and primitive or very primitive characters: they represent the so-called "primitive angiosperms."

4. The biogeographical definition of Madagascar should rest on two concepts:

a. The "Grande Ile" is fundamentally a fragment of Africa; its biota, taken

as a whole, is obviously an African one. Dejardin et al. (1973) said that this idea is now a classic one, and I agree. According to the estimates of Perrier de la Bâthie (1936), accepted by Humbert, the African element in the Madagascan flora would be around 27%, the pantropical and Asian elements being respectively 42% and 7%. The austral element contributes 3% and the recent element whose transport is due to long-distance dispersal, 15%. The remaining 6% represents the true Madagascan element. The studies of Dejardin et al. (1973) have complemented earlier ones. In particular, they recognize the existence of a neotropical element. Besides, they unite the pantropical and the "recent exotic" elements which Perrier had separated. Further, they add a seventh element, namely the palaeotropical one, which they subdivide. Thus, as one sees, their analysis goes much farther than the previous ones.

However, such a recognition of groups of elements and of percentages does not account for several essential factors.

What precise significance is to be given to these elements which we think are arbitrarily delimited? Their interrelationships should be analyzed more thoroughly. Insofar as Madagascar is a part of Africa, a Madagascan element is *ipso facto* an African one. Let us for example take the genera *Garcinia* and *Rheedia*, which Dejardin et al. (1973) have classified, respectively, in the palaeotropical element and neotropical element. These genera are in fact, not at all clear-cut and could be merged into one genus, which would then be a pantropical one. This case shows that any judgement concerning floristic affinities if founded on percentages of composition depends greatly upon taxonomic concepts. Moreover, the mere report of a common occurrence of a taxon in several areas may not reveal the true situation. In their paper, Dejardin et al. place *Symphonia* with neotropical elements, although it is in fact a genuine Madagascan one. Further, they reduced the Madagascan element to the endemic one. So, for Dejardin et al. terms such as "Madagascan element" and "endemic element" are synonymous. In fact, many so-called pantropical or palaeotropical or neotropical genera really belong to Madagascan stock. Although they are strictly Madagascan elements, they occur also in other areas.

b. Madagascar is a fragment of Africa, but it represents with its neighboring islands and eastern and southern Africa, a natural entity to which could be given the name "Madagascan region sensu lato." A number of reasons can be given to support this concept:

—A number of genera are common to eastern and southern Africa and Madagascar.

—Madagascar and the eastern coasts of Africa are the western border of the Indian Ocean.

—Madagascar, eastern and southern Africa were linked together, even though possibly separated by the sea, at the time when Gondwanaland was in existence.

—The uplift of the central mountain range in Africa during Tertiary times and the climatic changes in relation to this event increased the barrier between western and eastern Africa so as to reinforce the isolated position of all the eastern territories of which Madagascar is one part.

It is well known (Lebrun, 1961; Perrier de la Bâthie, 1936; Aubréville, 1955; Dejardin et al., 1973) that the African tropical flora must be divided into two parts, the Guineo-Congolese one having almost no affinity with the Madagascan one, and the Sudano-Zambezian flora whose relationships with the Madagascan one are very important. The strong disjunction is rather between the two African parts, than between Africa and Madagascar.

I shall now give a summary of the more significant taxa which support the concept of a close relationship between the floras of Madagascar and eastern and southern Africa. After that, I shall briefly survey the whole of the Madagascan flora by considering each family, except some unrevised ones, in its turn.

CLOSE RELATIONSHIPS BETWEEN THE FLORAS OF MADAGASCAR AND EASTERN AND SOUTHERN AFRICA

1. Families, subfamilies or tribes confined to the Madagascan region sensu lato and having at least one representative on either side of the Mozambique channel:

Myrothamnaceae (a monotypic family extending somewhat up to Zaïre) allied to the Hamamelidaceae and, possibly, to Didymelaceae, Hydrostachyaceae (we need detailed research on these two austral families, which were considered as primitive and linked within Pittosporales (suborder Brunineae) by Thorne, 1975; but the Hydrostachyaceae are placed in the Scrophulariaceae by Cronquist, 1968), Ptaeroxylaceae, Androstachyaceae.

2. Families or groups of plants with wide distributions represented in the Madagascan regions sensu lato but not elsewhere in Africa:

Winteraceae (a subfamily in Madagascar), Canellaceae, Hamamelidaceae, Moringaceae, Cunoniaceae, Brexiaceae, Proteaceae, Myoporaceae, Velloziaceae.

3. Some families or tribes of wide distribution, including West Africa, but characteristically of the Madagascan region sensu lato:

Monimiaceae, Montiniaceae, Meliaceae—Turraeeae, Portulacaceae, Palmae—Borassoideae, Pandanaceae, Poaceae—Bambuseae.

4. Some genera confined to the Madagascan region sensu lato (having at least one species on either side of Mozambique channel):

Otoptera (Leguminosae, 1 sp. in S. Africa, 1 sp. in Madagascar); *Xanthoceris* (Leguminosae, 1 sp. in S. Africa, 1 sp. in Madagascar); *Thilachium* (Capparaceae, 20 spp., 9 of which are in Madagascar and the Mascarene Islands, 1 sp. nonendemic); *Calantica* (Flacourtiaceae, 5–7 spp. in Madagascar and possibly in E. Africa, Airy Shaw, 1966); *Apholia* (Flacourtiaceae, 4–5 spp. or only 1 polymorphic species which reaches E. Africa, Airy Shaw, 1966); *Ludia* (Flacourtiaceae, 7 spp. in Madagascar and possibly in E. Africa, Airy Shaw, 1966); *Cassinopsis* (Cellastraceae, 2 spp. in S. Africa, 4 spp. in Madagascar, all endemic); *Hyalocalyx* (Turneraceae, 1 sp. in Madagascar and Mozambique); *Sparmannia* (Tiliaceae, 1 sp. in S. Africa, 1 sp. common in Madagascar and E. Africa, 1 sp. in Madagascar; this genus belongs to an entirely African tribe); *Gossypioides* (Malvaceae, 1 sp. in

E. Africa and Madagascar); *Dais* (Thymelaeaceae, 1 sp. in E. and S. Africa, 1 sp. in Madagascar); *Sphedamnocarpus* (Malphighiaceae, 1 sp. endemic to S.W. Africa, 15 spp. in Madagascar); *Lepidotrichilia* (Meliaceae, 1 sp. in E. Africa, 3 spp. in Madagascar); *Erythrophysa* (Sapindaceae—Koelreuterieae, 3 spp. in E. Africa, 6 spp. in Madagascar); *Macphersonia* (Sapindaceae—Schleichereae, several species in E. Africa-Madagascar); *Camptolepis* (Sapindaceae—Schleichereae, 1 sp. common to E. Africa and Madagascar, 2 spp. in Madagascar); *Stadmannia* (Sapindaceae-Nephelieae, 1 sp. common to the Mascarene Islands, Madagascar and E. Africa: *S. oppositifolia*; Capuron has described 5 Madagascan species representing a very distinct group, flowers of which are dioecious and with petals); *Protorhus* (Anacardiaceae, 1 sp. in S.W. Africa, 20 spp. in Madagascar); *Rhoicissus* (Vitaceae, 10 spp. in E. Africa, one of which reaches the Comores Islands); *Rhigozum* (Bignoniaceae—Tecomeae, 3 spp. in S. Africa, 1 sp. in Madagascar); *Hydnora* (Hydnoraceae, 10 spp. in S. and E. Africa, only 1 sp. in Madagascar, which represents a section of its own, *Neohydnora*; the other genus *Prosopanche* of this bitypic family is endemic to S. America—Paraguay, Argentina); *Kniphofia* (Liliaceae, many spp. in E. and S. Africa, 1 sp. in Madagascar); *Geissorrhiza* (Iridaceae, many spp. in S. Africa, 2 spp. in Madagascar); *Gonioma* (Apocynaceae—Alstonieae, 1 sp. in S. Africa, 1 sp. in S.W. Madagascar, Markgraf, 1976); *Mascarenhasia* (Apocynaceae—Mascarenhasiinae, a monotypic tribe; 12 spp. in Madagascar, 1 of which reaches E. Africa); *Pachypodium* (Apocynaceae—Pachypodiinae, a monotypic tribe; a genus with 17 spp., 12 of which are in Madagascar, the other species are in S.E. and S.W. Africa); *Hazunta* (Apocynaceae—Tabernaemontanoideae, 7 spp. in Madagascar, 1 of which extends to E. Africa, *H. coffeoides*); *Uncarina* (Pedaliaceae; it is the single genus of the Pedaliaceae endemic to Madagascar; this genus is closely allied to *Harpagophyton* of S. and E. Africa); *Medemia* (Palmae, 3 spp. in N.E. Africa and Madagascar).

5. Some genera characteristically of the Madagascan region sensu lato but nonendemic to this region and absent from western Africa:

Ocotea (Lauraceae, 270 spp. in America, several spp. in S.E. Africa, 16 spp. in Madagascar; *Ocotea* could have some distant affinity with *Hypodaphnis* a monotypic genus of W. Africa); *Hirtella* (Chrysobalanaceae, 100 spp. in tropical America, 1 in E. Africa, 4 spp. in Madagascar—3 endemic—1 sp. common to E. Africa and Madagascar; this genus is related to the Madagascan endemic genus *Grangeria*); *Carpodiptera* (Tiliaceae, 3 spp. in Cuba and West Indies, 1 sp. in E. Africa and Madagascar); *Piriqueta* sect. *Erblichia* (Turneraceae, 1 sp. in Central America, 1 sp. in southern Africa, 3 spp. in Madagascar; the genus *Piriqueta* is greatly diversified in America; a Madagascan species, *Piriqueta integrifolia*, is an isolated taxon whose status needs restudy); *Vepris* (Rutaceae, 20 spp. in S. and E. Africa, 24 spp. in Madagascar); *Tristellateia* (Malpighiaceae, a palaeotropical genus with 20 spp. in Madagascar, 1 sp. in E. Africa); *Nesogenes* (Verbenaceae, 6 spp.; this genus, closely allied to the Madagascan endemic genus *Acharitea* (1 sp.), has one endemic sp. in Madagascar, the other species being in E. Africa and Polynesia; these two genera belong to a group, a family of its

own according to some authors [Dicrastylidaceae], which is essentially Australian; they are closely related to the Verbenaceae—Stilboideae, a small subfamily of 5 monotypic genera, endemic to S. Africa); *Dicoma* (Compositae—Mutisieae, 35 spp. in E. and S. Africa, 1 sp. in tropical Asia, 4 spp. in Madagascar, all endemic); there are many genera in the Compositae—Inulae with a comparable distribution: *Polycline*, *Athrixia*, *Iphiona*, *Humea*, *Brachylaena*, *Stenocline*, etc.).

6. Some genera characteristically of the Madagascan region sensu lato, nonendemic to this region and weakly represented in tropical West Africa:

Buxus (Buxaceae, 6 spp. in S. and E. Africa and Madagascar, 1 sp. belonging to another group in W. tropical Africa); *Delonix* (Leguminosae, a genus of several spp. in Madagascar and E. Africa); *Commiphora* (Burseraceae, a genus with many spp. of warm Africa and India; some spp. in W. tropical Africa, more than 20 spp. in E. Africa, even more in Madagascar); *Philippia* (Ericaceae, 40–50 spp. in Madagascar, 10 spp. in E. and S. Africa, 1 sp. on Mt. Cameroon); *Vaccinium* (Ericaceae, some spp. in Madagascar, many in S. Africa but none on mountains in tropical Africa); *Dombeya* (Sterculiaceae, 200 spp., 20 of which are in E. and S. Africa and a few elsewhere in tropical Africa); *Gravesia* (Melastomataceae, 100 spp. in Madagascar, 7 of which are common to E. Africa, 2–3 spp. in W. Africa); *Mimusops* (Sapotaceae, a genus of 18–19 spp. in Madagascar, the Comores, Mascarene and Seychelles Islands, 12 in E. and S. Africa, only 2 in W. Africa); *Sphaerothylax* (Podostemaceae, 1 sp. in Cameroon, 1 in S. Africa, reaching Angola and Zambia, 1 in E. Africa, Ethiopia, and Madagascar); *Kalanchoe* (Crassulaceae, 1 section in S. Africa, 3 sections in Madagascar—Dejardin et al., 1973); *Streptocarpus* (Gesneriaceae—Cyrtandroideae, a genus of many species in S. and E. Africa, some 40 spp. in Madagascar—where a genus closely allied, *Colpogyne*, is confined—some spp. in W. tropical Africa); *Helichrysum* (Compositae—Inulae, a palaeotropical genus of 500 spp.—extending to Australia—of which over 100 occur in Madagascar and 200 in S. Africa); *Stoebe* (Compositae—Inulae, 30 spp. in S. Africa, 1 sp. in Angola, 1 in Rhodesia, 2 spp. endemic to Madagascar, 1 sp. endemic to Réunion); *Aloe* (Liliaceae, a genus well developed in Madagascar, where it has 30 endemic spp. also in E. and S. Africa); *Coleotrype* (Commelinaceae, 5 spp. in Africa and Madagascar).

7. The littoral formations, mangroves included, along east African coasts also offer characteristic features of the Madagascan region. These formations are composed of plants unknown on the Atlantic coast such as *Barringtonia racemosa*, *Sonneratia alba*, *Lumnitzera racemosa*, *Bruguiera gymnorhiza*, *Rhizophora mucronata*, *Ceriops tagal*, *Heritiera littoralis*, *Xylocarpus* (the two species) and *Cycas thouarsii*. A few mangrove species of Madagascar do not reach the African coast, but many other species of the oriental mangroves reach neither the Madagascan coast, nor the eastern African one. The Madagascan mangrove flora is a typical oriental flora, but a strongly impoverished one.

Biogeographical Survey of the Madagascan Flora
(Families are arranged roughly according to Cronquist's system)

I

Winteraceae (8 gen., 57 spp.), which are clearly among the most primitive families of the angiosperms, are represented in Madagascar by a unique species, the so-called "*Bubbia*" *perrieri*, which is the single representative of the family in Africa-Madagascar. The other genera but one are concentrated in some Pacific islands and Australia: *Pseudowintera* (3 spp. in New Zealand); *Exospermum* (1 sp. in New Caledonia); *Bubbia* (30 spp. in New Caledonia, New Guinea, and Australia); *Belliolum* (4 spp. in New Caledonia, 4 spp. in the Solomon Islands); *Zygogynum* (6 spp. in New Caledonia); *Tasmannia* (5 spp. from Malesia to Australia, a genus often treated as a subgenus of *Drimys*); and *Drimys* (4 spp. in S. America–Mexico).

The Madagascan species wrongly described as *Bubbia* is indeed a quite different genus, and I proposed (Leroy, 1977a) considering it as a subfamily of its own. Thus, the distributional pattern of the Winteraceae is not only typically austral, but the Madagascan species bears witness that the Madagascan region is a part of what was the cradle of the *Winteraceae*; therefore, a part of the cradle of primitive angiosperms.

But more is to be said. "*Bubbia*" *perrieri* has an advanced gynoecium that is a pseudo-monomerous ovary composed of 2 carpels united and opened, a type only known in two families in the order Magnoliales, the Annonaceae—Monodoroideae and the Canellaceae. Let us not forget that all of these plants occur in one and the same area, except for the Canellaceae which occur also in tropical America. The Winteraceae, which have no representative in Africa, and the Canellaceae form an integral whole because of their close relationships, and they should not be too separated.

Annonaceae 125 gen., only 9 of which are represented in Madagascar: 1 endemic, *Ambavia* (2 spp.); 3 African-Madagascan, *Isolona* (19 spp., 5 in Madagascar), *Monanthotaxis* (some spp. in Africa and Madagascar), *Hexalobus* (6 spp., 1 in Madagascar); 4 palaeotropical, *Uvaria* (120 spp., 15 in Madagascar), *Artabotrys* (100 spp., 6 in Madagascar), *Polyalthia* (100 spp., 15 in Madagascar), *Popowia* (50 spp., 16 in Madagascar); 1 pantropical, *Xylopia* (100 spp., 25 in Madagascar). All but some of the species (the total number of which is 100) are endemic.

Annonaceae are rather poorly represented in Madagascar. As a whole, their affinities are palaeotropical and especially African. A remarkable fact is that the subfamily Monodoroideae, principally characterized by a compound ovary, and composed of 2 genera (*Isolona* in Africa and Madagascar, and *Monodora* in Africa), palynologically akin (Walker, 1971), is endemic to Africa-Madagascar.

Myristicaceae (16 gen., 5 of which in America—Uphof, 1959—300 spp.). This family is represented in Madagascar by 3 endemic genera (Capuron, 1972a, 1973b): *Haematodendron* (1 sp.), *Brochoneura* (3 spp.), and *Mauloutchia* (6 spp.); in tropical Africa by 4 endemic genera; in tropical Asia by 4 endemic genera. Taking the family as a whole, almost 50% of the genera are African-

Madagascan. None of them is pantropical. The Madagascan genera, like the African ones, have few species, always less than 7.

Furthermore, the genus *Haematodendron* is, as compared to the others, strongly differentiated with some very primitive characters (stigma sessile, subapical-lateral, slightly oblique, with two well-marked papillose lips, separated by a sutural groove which nearly extends down to the bottom of the carpel; therefore, certainly a monomerous ovary!) and some very advanced characters (plants dioecious, flowers with united sepals, ovary stipitate, seeds exarillate, albumen ruminate).

So it is easy to assign a Gondwanian origin to this very archaic family, whose specific differentiation has been active in America (Smith & Wodhouse, 1938) and, above all, in Asia. The African-Madagascan genera appear to be isolated survivors with few species.

The *Canellaceae* is a small tropical and subtropical family of 5 genera (11 spp.) whose distribution is restricted to America and Africa. Genera are endemic to any parts of the region: 3 of them in America; 1 in S. Africa; 1 in Madagascar: *Cinnamosma* (3 spp.). The most striking fact is that the family is a very natural one and closely allied to the Winteraceae: they have partly the same distributional pattern and the same ovarian type (Leroy, 1977a). It is probable that they have had a common ancestor (with a monosulcate pollen, which is the one of present Canellaceae, and free carpels), which inhabited Gondwanaland.

The *Monimiaceae* (25 gen.) is one more example of a panaustral family almost absent from the Guineo-Congolese flora, but richly represented in the Madagascan region sensu lato. There is a strong concentration of endemic genera in Madagascar and the Mascarene Islands, possibly 6: *Ephippiandra* (1 sp.); *Phanerogonocarpus* (2 spp.); *Decarydendron* (1 sp.); *Hedycaryopsis* (1 sp.); *Monimia* (4 spp.); *Tambourissa* (26 spp.). Two genera are recognized in Africa: *Xymalos* (2–3 spp.) almost restricted to E. and S. Africa but reaching Mt. Cameroon; *Glossocalyx* (3–4 spp.) confined to the Guineo-Congolese flora. The latter genus is strongly differentiated and often considered as the single African member of the separate family Atherospermataceae. According to Hutchinson (1964), no representative of the Monimiaceae occurs in Africa, since he places *Xymalos* in the Trimeniaceae. Two other genera of Monimiaceae have been seen as types of separate families. It has been proposed that *Hortonia* of Ceylon be raised to the family level, a status which is generally granted to *Amborella* of New Caledonia. In spite of the unsatisfactory taxonomic treatment applied to the Monimiaceae, it is clear that this group of related plants, which is widely dispersed in the Southern Hemisphere, is characterized by its discontinuous area, the morphological isolation of certain genera, and its near absence from Africa.

Lauraceae (35–40 gen., 2,000 spp. tropical & subtropical). This primitive family is very poorly represented in Africa-Madagascar, but its distribution offers a great interest. Aside from the parasitic vine *Cassytha filiformis*, present in both Africa and Madagascar, there are 4 genera in continental Africa, of which one is an endemic monotypic genus (*Hypodaphnis*) and belongs to a tribe of its own.

Beilschmiedia, a pantropical genus of 200 species, with 80 species in Africa, is absent from Madagascar. Two genera, *Ocotea* and *Cryptocarya*, are common to Africa and Madagascar; the latter is a large American genus with 8 species in Madagascar and some species restricted to E. and S. Africa. The American genus, *Ocotea*, has 18 species in Madagascar, and only a few in tropical and E. and S. Africa. There are 3 other genera in Madagascar: *Ravensara*, an endemic genus (18 sp.) related to *Cryptocarya* (Cryptocaryeae); *Potameia*, a genus with many Madagascan species (19) and a few (3) in tropical Africa; *Apollonias*, a widely spread genus with 6 endemic species in Madagascar, absent from continental Africa but present in the Canaries (with *Persea* and *Laurus*).

It is to be noted that the tropical African center is very poorly provided with genera of Lauraceae, the chief centers of distribution being S.E. Asia and S. America. The family is better represented in the adjoining islands (Canaries, Madagascar) than on the continent.

Hernandiaceae. This small pantropical family of 4–5 genera and 60 species has a typically austral distribution. It is of the utmost theoretical importance in that it offers not only an austral distribution, but also a wide range of isolated genera with many very primitive characters. There is undoubtedly evidence for a Gondwanian origin of the whole family (Kubitzki, 1969). Hernandiaceae are represented in Madagascar by 4 genera: *Hernandia* subgen. *Hernandia* (2 spp., 1 of which is endemic; 1 sp. endemic to the Mascarenes); *Hazomalania* (*Hernandia* subgen. *Hazomalania* (Capuron, 1966b; Kubitzki, 1969) (1 sp.); *Illigera* (1 endemic sp.); *Gyrocarpus* (1 sp., *G. americanus*). According to Kubitzki, most primitive components occur in Australia (*Hernandia* subgen. *Valvanthera*) and Madagascar (*Hazomalania*). The fifth genus, *Sparattanthelium*, is endemic to tropical America. Kubitzki has divided *Gyrocarpus*, a pantropical genus dispersed by sea currents, into 8 species, 3 of which are endemic to Madagascar; it, almost certainly, belongs to the mechanism of diffenentiation to which such species as *Calophyllum inophyllum* are also answerable.

Chloranthaceae. This small family is of exceptional interest for both its morphological characters, some of them being very primitive, and its distributional pattern. If the Madagascan genus *Ascarinopsis* (Humbert & Capuron, 1955) (1 sp.) is reduced to *Ascarina*, of which, at the best, it could be a special section, the Chloranthaceae is composed of 4 genera, which are, of course, related with one another, but only distantly, and their distributional area is extremely discontinuous. And what is more, the only genus *Hedyosmum*, which has 40 species in tropical America and the West Indies, and 1 species in S.E. Asia, represents a strongly differentiated, isolated line with at least special subfamily status. In particular, it offers evolutionary characters some of which are most advanced and some others most primitive. It seems its distribution might have resulted, more or less recently, from a post-Gondwanian extension. The other 2 genera are: *Chloranthus* (15 spp., in E. Asia and Indomalaysia) and *Sarcandra* (3 spp. in the same area). Obviously, I agree with Smith (1972) that the present genera of Chloranthaceae are only a few remnants of an old, large Angiosperm flora which has almost entirely disappeared from the earth. With this interpretation the presence of one *Ascarina* species in Madagascar has no clear significance,

as the species may have come by long-distance dispersal at any time during the Tertiary.

Piperaceae, *Aristolochiaceae*, *Nymphaeaceae*, *Ceratophyllaceae*, *Ranunculaceae*, *Papaveraceae* (cf. Humbert, 1959).

Menispermaceae (65 gen., 350 spp., chiefly in the tropical Old World). They are particularly well represented in Africa with 21 genera, 12 of which are endemic, and 65 species. There are perhaps 12 genera in Madagascar, 5 of which are endemic (*Orthogynium*, *Burasaia*, *Rhaptonema*, *Spirospermum*, *Strychnopsis*). Two genera are common to Madagascar and Africa (*Anisocycla*, *Triclisia*). To summarize, 19 genera are endemic to Africa-Madagascar and the remainder, except for 2, are palaeotropical. There is no direct link with America. This pattern of distribution, typically Gondwanian, poses a major problem because the other families in the order Berberidales are without doubt Laurasian.

II

Hamamelidaceae. This family, composed of 22–25 genera and about 100 species, ranges from S. and N. America to Australia, but occurs principally in S.E. Asia; it has 2 elements in Africa and Madagascar: *Dicoryphe* in Madagascar with 15 species and *Trichocladus* in tropical E. Africa and S. Africa with 5 species. According to Hutchinson this pattern of distribution resembles that of Magnoliaceae. There are however some interesting differences in that the latter family is absent from Australia and Africa and present in S. America. In spite of their very strong diversification in the Northern Hemisphere, principally in S.E. Asia, Hamamelidaceae are characterized by a widespread and discontinuous distribution that includes Africa and Australia. This pattern of distribution provides evidence of primitiveness and possibly that Hamamelidaceae might have originated in Gondwanaland according to one of two hypotheses envisaged by Raven & Axelrod (1974).

Myrothamnaceae is a monotypic family with 2 closely related species: one endemic to Madagascar, the other in E. and S. Africa (but also in Angola, Zambia and S. Zaïre).

Hydrostachyaceae. A monotypic family with the same pattern of distribution as the previous one, but with many species (18 endemic spp. in Madagascar, some 30 in S. Africa).

We need detailed researches on these small austral families considered as primitive and bunched together within Pittosporales (suborder Brunineae) by Thorne (1968, 1975), but the Hydrostachyaceae are placed in the Scrophulariales by Cronquist (1968).

Didymelaceae. A monotypic family of 2 species endemic to Madagascar whose taxonomic position is still uncertain. It is a rather primitive taxon (with solitary carpel and scalariform perforations) considered sometimes as close to Euphorbiaceae or Hamamelidales, or sometimes as an order of its own (Takhtajan, 1969).

Myricaceae. (4 gen., 40 spp.). This family, which is widely dispersed in temperate regions and tropical mountains of both hemispheres, is divided into two

subfamilies, one of which, monotypic and very archaic, the Canacomyricoideae, is endemic to New Caledonia (Leroy, 1949, 1957). The genera *Comptonia* (endemic to N. America, with 1 sp.), *Gale* (1 sp. in the Northern Hemisphere), and *Myrica* (temperate and tropical zones) are closely allied. The family is present in S. America, in Africa (many spp. in S. Africa), and in Madagascar with the genus *Myrica* (6 spp.).

Myricaceae is generally considered as a Laurasian family, but two facts argue against this view. First, the tropical distribution of *Myrica*, and, in particular, its abundance in S. Africa. Second, the existence of *Canacomyrica* in New Caledonia, where it certainly is a completely isolated survivor. *Comptonia* and *Gale* are possibly Laurasian segregants, but *Myrica* and, above all *Canacomyrica*, might indicate greater antiquity.

Moraceae. This family divided into 3 subfamilies (Moroideae, Artocarpoideae, Conocephaloideae), 75 genera, and 2,000 species is widespread in warm regions and the tropics and is represented in Madagascar by 11 genera and 42 species. If, following Hutchinson's division, we accept 9 tribes, all of them are represented in Madagascar, each of them by one or two genera (the small subfamily Conocephaloideae being excluded). Fatoueae: *Fatoua*, a genus with only 2 species, of which 1 occurs in Madagascar, the other in Asia, New Caledonia. Dorstenieae: *Dorstenia*, a pantropical genus with 100 species of which 2 occur in Madagascar. Strebleae: *Streblus*, a palaeotropical genus with 4–5 species, of which 1 occurs in Madagascar; *Maillardia*, an endemic genus with 4 species. Moreae: *Ampalis* and *Pachytrophe*, 2 endemic and monotypic genera. Broussonetieae: *Allaeanthus*, an endemic and monotypic genus. There are 4 genera in the Artocarpoideae: Euartocarpeae: *Treculia*, an African-Madagascan genus with 12 species of which 4 occur in Madagascar. Brosimeae: *Bosqueia*, another African-Madagascan genus with 12 species, of which 7 occur in Madagascar. Olmedieae: *Antiaris*, a palaeotropical genus with 10 species, of which 2 occur in Madagascar. Ficeae with 16 species in Madagascar.

The Madagascan Moraceae offer a basis for some interesting comments. First, we have to emphasize that the whole family is represented in Madagascar by all the tribes. Even the endemic genera are distributed into 3 tribes. Judging from these facts, one has good justification to uphold the hypothesis of Madagascar as a center of survival. Second, since there are 4 endemic genera, 2 African-Madagascan ones and 3 palaeotropical ones, links with America are weak. Third, it is noteworthy that the tribe Moreae, represented by 2 endemic genera, has no representative of *Morus*, a widespread genus, one subgenus of which occurs in tropical Africa, another in Asia, and yet another in America.

Urticaceae. A family of 50 genera (800 spp.) mostly in warm regions and tropics, is particularly well represented in America. There are 14 indigenous genera in Madagascar, one of which, *Neopilea* (2 spp.) is endemic, and 51 species (41 endemic) occur on the island.

As with the Moraceae, all tribes (5) of Urticaceae are represented in Madagascar, but endemism is weak, and pantropical or widespread genera are as many (6 in number) as palaeotropical ones. There is also an American-Madagascan genus, *Phenax*, with 20 species in America and 3 in Madagascar and the

Mascarenes. Further, one palaeotropical genus, *Pipturus*, reaches the Comores (1 nonendemic sp.) but neither Madagascar nor Africa.

Ulmaceae (15 gen., 150 spp.). This family has 4 genera in Madagascar: *Celtis* (3 Madagascan spp.; 1 of which is palaeotropical, the other 2 are related to African species); *Trema* (2 Madagascan spp., 1 of which is endemic with eastern affinities); *Aphananthe* (1 sp., endemic; the genus is closely related to *Celtis*); *Chaetacme* (1 African-Madagascan sp.).

Casuarinaceae (cf. Humbert, 1959).

III

Nyctaginaceae (cf. Humbert, 1959).

Phytolaccaceae (12 gen., 100 spp.). A family particularly well represented in America and S. Africa. Four genera are present in Madagascar, 1 of which, *Barbeuia*, is endemic, monotypic, and morphologically isolate (ovary 2-carpellate, syncarpous, 2-loculary). There is an endemic species of *Phytolacca*.

Didiereaceae. This remarkable family, endemic to South and Southwest Madagascar, consists of 4 genera: *Decaryia* (1 sp.); *Alluaudiopsis* (2 spp.); *Alluaudia* (6 spp.); *Didierea* (2 spp.).

Didiereaceae, certain of which have a habit resembling American Fouquieriaceae, are, with arborescent aphyllous euphorbias, the most striking feature of the southern Madagascan vegetation; it recalls somewhat the Brazilian "Caatinga" (Koechlin, 1972). According to Rauh's work (Rauh & Reznik, 1971), the family has definite affinities with the American family Cactaceae and must be placed in Centrospermae.

Cactaceae. It is a family of many genera, perhaps over 100, and 1,500 species almost wholly American. *Rhipsalis*, the single genus with representatives outside America, has one species, *R. baccifera* (J. S. Mill.) Stearn in tropical Africa, Ceylon, and Madagascar. And what is more, the Madagascan plant is so variable that several species have been described. According to Guillaumet (1972) there are at least two well characterized forms, each of them inhabiting a special ecological region: *R. horrida* (eastern littoral forest) and *R. suarezensis* (western Domain). This pattern of distribution has given rise to discussions, but it is probable that this differentiation has originated secondarily. A study of the whole genus *Rhipsalis* is needed before any opinion can be attempted.

Aizoaceae (*Molluginaceae* included) (130 gen., 1,200 spp., chiefly S. African). This unrevised family has some nonendemic genera in Madagascar (*Mollugo*, *Sesuvium*, *Trianthema*, . . .) with about a dozen species (Baron, quoted by Humbert, 1959).

Caryophyllaceae. This family is represented by 7–8 nonendemic genera (subfamily Alsinoideae) and 11 species, 8 of which are endemics. There are 2 endemic species of the palaeotropical genus *Corrigiola* and 5 species of the tropical and subtropical genus *Polycarpaea* (Perrier de la Bâthie, 1936).

Portulacaceae. This is a very interesting family of about 20 genera, most of them American. But 7 genera occur in Africa sensu lato, 4 of them endemic to Madagascar: *Talinella* (2 spp.), or South Africa: (*Ceraria*, 4 spp.; *Portulacaria*,

2 spp.; *Calyptrotheca*, 2 spp.) (Brenan, 1949; McNeill, 1974). The genus *Anacampseros* (50 spp.) is common to S. Africa and Australia. The genera *Portulaca* and *Talinum* are represented; the former in Madagascar (3 spp.), the latter in the Mascarenes (1 sp.). Although the family has two main centers of distribution, S. America and western N. America, it is as a whole a rather austral one. Moreover, it is closely related with the large family Aizoaceae, absent from Madagascar, but primarily represented in S. Africa. With respect to Portulacaceae, Madagascar and Australia look as if they were parts of a borderland.

Basellaceae, *Chenopodiaceae*, *Amaranthaceae*, *Polygonaceae*, *Plumbaginaceae* (cf. Humbert, 1959).

IV

Dilleniaceae (10 gen., 400 spp.). This family is represented in Madagascar by 3 nonendemic genera: *Hibbertia*, a genus of 155 species, 130 of which are in Australia, 24 in New Caledonia and Fiji, 1 (*H. coriacea*) in Madagascar (this one is closely related to Australian species); *Tetracera*, a pantropical genus of 50 species with 3 species in Madagascar, all of them endemic, and about 10 species in Africa. *Dillenia*, an Asian-Australian genus of 60 species, 1 of which, nonendemic is in Madagascar, and another endemic to the Seychelles. Apart from *Tetracera*, none of the genera of Dilleniaceae occur in Africa. According to Hutchinson there is one more genus, endemic to the Seychelles (*Neowormia*), related to *Dillenia*. Let us also not forget that the genus *Schumacheria* (3 spp.) is endemic to Ceylon. One must, it seems, put apart *Hibbertia*, which may have arrived by long-distance dispersal. But with *Neowormia* and *Schumacheria* we have possibly an indication of a much more ancient settlement for the family. Besides, the pantropical genus *Tetracera* belongs to the tribe Delimeae, largely American. One feels as if the Dilleniaceae, almost absent from Africa today, must have been much more numerous in the past and would have become extinct during the Tertiary. We are also badly in need of a detailed monograph of this especially interesting family.

Ochnaceae. (30 gen., 250 spp.) is an almost entirely tropical family, especially well represented in S. America. Its Madagascan representatives, which belong to subfamily Ochnoideae, tribe Ochneae (Kanis, 1968), are: *Ochna*, a palaeotropical genus of about 100 species in Africa south of the Sahara, Arabia, Madagascar, the Mascarenes, and 4 species in tropical Asia with perhaps 20 endemic species in Madagascar. *Gomphia* (= *Campylospermum*), a palaeotropical genus of 12 species, of which 5 are endemic to Madagascar, and 3 in Africa. *Brackenridgea* (= *Pleuroridgea*), another palaeotropical genus, containing 10 species, of which 2 endemic to Madagascar.

It is striking that there is no endemic genus. With the Madagascan Ochnaceae we deal with a part of a palaeotropical group, even though the family is chiefly South American.

Diegodendraceae (1 gen., 1 sp.). An endemic family (Capuron, 1963b).

Sphaerosepalaceae. This is an endemic family of Madagascar which consists of 2 genera of woody plants: *Rhopalocarpus* (15 spp.) and *Dialyceras* (3 spp.).

The best place for this family seems next to Diegodendraceae within Ochnales, but there are also links with Malvales.

Sarcolaenaceae (10 gen., 35 spp.). An endemic family.

Elatinaceae (2 gen., 45 spp.) (cf. Humbert, 1959).

Guttifereae and *Hypericaceae* represent a chiefly tropical group of 1,000 species in 40 genera, of which 8 are endemic to Africa-Madagascar. If we put aside *Hypericum*, an herbaceous genus of wide distribution throughout temperate regions and tropical mountains, 2 genera offer a widespread distribution: *Garcinia* and *Calophyllum*. However, both are far more highly differentiated in Asia-Australasia than in America or Africa; *Calophyllum*, which has 16 Madagascan species, is completely absent from Africa. *Symphonia* is abundantly diversified in Madagascar with many species or "morphological entities" merging into one another, but there are also 1–2 species in Africa and America. Its affinities are with *Montrouziera* of New Caledonia. Twenty species or so of *Mammea* inhabit Madagascar, all of them endemic, over 20 other ones occur in Asia-Indonesia, extending to New Guinea, except for Australia, but only 1 is met in Africa and another in S. America.

There are 3 endemic genera: *Eliaea*, related to the Asian genus *Cratoxylum*, *Ochrocarpos*, and *Paramammea* (Leroy, 1975, 1977b), each of them belonging to a different tribe. Finally, the other 2 genera, *Harungana* and *Psorospermum*, are common to Africa and Madagascar.

From these data, which are difficult to understand, one can however draw some conclusions:

Guttifereae are comparatively better represented in Madagascar than in Africa. The affinities between certain genera such as *Mammea-Paramammea* on the one hand, and *Garcinia-Ochrocarpos* on the other hand, show that these genera are probably not newcomers and that they probably differentiated there.

Such genera as *Symphonia* and *Mammea* look as if they had originated and evolved in Madagascar, although their affinities are with Asian-Pacific genera.

There is some evidence that as a whole, the Guttifereae-Hypericaceae of Madagascar and Africa may have differentiated there, when S. America, Africa, and Australia were no longer in contact.

The fact that 14 endemic species of *Calophyllum* (Stevens, 1976) occur in Madagascar, the genus being unknown in Africa, poses a problem. According to Perrier de la Bâthie (1936) all of the Madagascan species are derived from the beach species *Calophyllum inophyllum*. There is a great need for thorough research in evolutionary biology of this very interesting problem. Whatever the answer will be, it is quite certain that *Calophyllum* has occurred there for a very long time.

Dipterocarpaceae. This family of 18 genera, which has until now been considered as a typically palaeotropical one, has at least one representative (a monotypic subfamily) in Guyana (Maguire et al., 1977). It is basically divided into 2 very distinct subfamilies: Dipterocarpoideae and Monotoideae. The former is Asian with 13 genera and 247 species in only Borneo, a number that quickly decreases going toward India where only 6 genera and 14 species occur. However, it is surprising enough to meet as many as 10 genera and 44

species in Sri Lanka (Ceylon). Moreover, one genus, *Vateriopsis*, is endemic to the Seychelles and several Tertiary fossils have been found in E. Africa (Aubréville, 1976a). The Monotoideae comprises 2 genera: *Monotes* with 1 endemic species in Madagascar, 1 species in western tropical Africa, and 40 species or so in dry tropical S. Africa; *Marquesia*, with 4 species in tropical Africa. Some Tertiary fossils of this subfamily have been described from the temperate Northern Hemisphere, but their identity is not always convincingly established.

One can perhaps presume that Dipterocarpaceae has been a pantropical family which has become particularly impoverished in Africa during the Tertiary era owing to geological and climate alterations. It would have found a center of survival in Southeast Asia which has also become a new center for development (Meijer, 1974). It is however noteworthy that the family is very poorly represented in Madagascar, and absent from Australia.

Theaceae: cf. *Asteropeiaceae*.

Asteropeiaceae. This unigeneric family, endemic to Madagascar, contains 5–6 species which occur both in the western and eastern parts of the country. It is of great interest due to its close affinities with Theaceae (Melchior, 1925), from which it is distinguished by minor characters; *Asteropeia* is clearly a relict. We have to emphasize that Theaceae are represented in Africa-Madagascar by only 2 species of the large genus *Ternstroemia* (Hepper, 1968; Letouzey, 1977b) and 2 genera endemic to Africa: *Melchiora* (3 spp.) and *Ficalhoa* (1 sp. ?).

Medusagynaceae. (An unispecific family endemic to the Seychelles.)

Elaeocarpaceae. This family (8 gen., 400 spp.) is closely allied to Tiliaceae, of which it is considered often as a subfamily or a tribe, and is typically of southern distribution (S. America, Australia, New Zealand, New Caledonia, New Guinea), the only genus *Elaeocarpus* reaching northward India, China, and Japan. Curiously enough, there are 2 endemic species of *Elaeocarpus* in Madagascar (though none in Africa) and 1 endemic species of *Sloanea*, a widespread genus (likewise absent from Africa). They "probably reached Madagascar by long-distance dispersal around the Indian Ocean" (Raven & Axelrod, 1974). One must not exclude, however, that this mechanism may have operated early in the Tertiary when Australia was closer to Africa.

Tiliaceae is a predominantly woody family (60 gen., 1,200 spp.) mostly of tropical and subtropical distribution. Following Capuron (1963a, 1964), 7 genera occur in Madagascar: *Christiana* (1 African-Madagascan sp.); *Carpodiptera* (1 sp. in E. Africa and Madagascar, 3 spp. in Cuba and the West Indies); *Sparrmannia* (1 Madagascan sp., 1 Madagascan-E. African, 2 S. African); *Grewia* (more than 400 spp. of the tropics and subtropics); *Pseudocorchorus* (a monotypic tribe Pseudocorchoreae, 6 spp.); *Corchorus* (6 spp., nonendemic); *Triumfetta* (5 spp., nonendemic).

We also have to note the singular bipolar distribution of the genus *Carpodiptera*, the distribution of *Sparrmannia*, a genus of an entirely African tribe, and the fact that *Christiana* is a morphologically very isolated genus. The family is curiously anchored on Madagascar with an endemic tribe. Madagascan Tiliaceae are, however, strongly linked to Africa of which they are only a part.

Sterculiaceae is a woody family (38 gen., 1,000 spp.; Hutchinson, 1967) widely distributed in the tropics and subtropics. Out of 11 tribes recognized by Hutchinson, 6 are present in the Madagascan region, containing 22 genera (250 spp.). The tribe Dombeyeae, which is wholly palaeotropical, is composed of 11 genera, of which 8 occur in the Madagascan region, 6 being endemic; the nonendemic genera are: *Dombeya*, common to Madagascar and Africa but far more diversified in Madagascar, and *Melhania*, a widespread genus extending to Africa, Asia, and Australia.

Another fact must be pointed out: it is that 3 genera offer a very restricted endemism: *Astiria* (1 sp.) and *Trochetia* (5 spp.) to Mauritius, and *Ruizia* to Réunion. A third remark is the very important development of the African-Madagascan genus *Dombeya* in Madagascar and the Mascarenes, where about 200 species have been described, that is four-fifths of the whole.

The tribe Helmiopsideae consists of 3 genera, 2 of which are endemic to Madagascar, the third, *Nesogordonia*, having 10–12 species, half of which are Madagascan, the other half African.

The tribe Hermannieae has 3 Madagascan representatives but is deprived, it seems, of any biogeographical significance. The genus *Keraudrenia* (Lasiopetaleae, 12 genera) has one species in Madagascar (a single and ancient herbarium number is known of this plant).

More interesting is the tribe Byttnericae with 2 genera indigenous in Madagascar: the pantropical *Byttneria* and the Asian-Australian *Rulingia* (25 spp.), one species of which is endemic to Madagascar.

Sterculieae is present with 1 pantropical genus, *Sterculia*, and 2 palaeotropical genera: *Firmiana* and *Pterygota*.

There are 2 genera of the palaeotropical tribe Tarrietieae: *Hildegardia* (2 spp. out of 7) and *Heritiera* (1 sp. out of 7).

In summary, such isolated representatives as *Keraudrenia* and *Rulingia* have possibly no particular meaning from a biogeographical point of view; as Raven & Axelrod have noted, these species probably reached Madagascar "by long-distance dispersal around the Indian Ocean."

But I want to emphasize some important facts: a very strong endemism of a part of the family in Africa-Madagascar (Dombeyeae, Helmiopsideae); a high degree of endemism in the Mascarene; the affinities of the Madagascan Sterculiaceae are with the palaeotropical flora. Many genera both monotypic or paucispecific and endemic, particularly in the Mascarenes, appear to be survivors.

Bombacaceae is a family of 31 genera and 225 species (Hutchinson, 1967), wholly woody and confined to the tropics, mainly the American ones. The Durioneae, generally considered as one of the primitive tribes, is Asian-Australasian, but the other tribes are either strictly American or represented in America. Bombacaceae are represented in Africa and Madagascar only by the tribe Adansonieae, with 15 species distributed in 4 genera: the palaeotropical *Bombax* (2 spp. in Africa), the endemic genus *Rhodognaphalon*, closely related, if not similar to the American *Bombacopsis*, with 6 species in Africa, and *Adansonia* which extends from Africa (1 sp.) and Madagascar (8 spp.) to Australia (1 sp.). A third genus (*Ceiba*, tribe Ceibeae, also exists in Africa, but

it is unanimously considered as an American newcomer. Judging from the present evidence, one may suggest a Gondwanian (South American-African) origin for the Adansonieae. A noteworthy fact recalled by Aubréville (1975a) is the African disjunction in the pattern of distribution concerning the whole family.

Malvaceae. This family (88 gen., 2,300 spp.) is world wide both in temperate and tropical regions. It is represented in Madagascar by 3 tribes: Malveae (5 gen., 17 spp.), Ureneae (3 gen., 5 spp.), Hibisceae (13 gen., 7 of which endemic, and 80 spp., 60 of which endemic). There are only 3 endemic species within Malveae (*Abutilon*—Bates, 1968) and 2–3 endemic species within Ureneae (*Pavonia*) in Madagascar-Africa. The tribe Hibisceae, which is composed of 29 genera (Hutchinson, 1967), is well represented in Madagascar and Africa, even better in Madagascar with 13 genera, of which 7 are endemic, than in Africa with 12 genera, of which only 3 are endemic. The only genus, *Hibiscus*, occurs abundantly in Madagascar with 45 species, 30 of which are endemic. The endemic genera are paucispecific and not always neatly separated: *Megistostegium* (3 spp.), *Perrierophytum* (9 spp.), *Humbertiella* (3 spp.), *Macrostelia* (3 spp.), *Humbertianthus* (1 sp.), *Helicteropsis* (2 spp.), *Jumelleanthus* (1 sp.). The genus *Gossypioides* (2 spp.) is endemic to E. Africa-Madagascar.

Such genera as *Cienfuegosia* (Fryxell, 1974) (America, Africa, Australia), *Kosteletzkya*, and *Thespesia* are represented respectively by 1, 7, and 1 endemic species. Two genera of Madagascan Hibisceae have no endemic species: *Abelmoschus* and *Gossypium*.

Nepenthaceae (1 gen., 80 spp.). The genus *Nepenthes* is confined to the Indian Ocean with 2 endemic species in Madagascar and 1 endemic in the Seychelles.

Droseraceae (1 gen., 90 spp.). Five species inhabit Madagascar, one of which endemic.

Lecythidaceae. Hutchinson (1964) has divided this family into two in accepting the Barringtoniaceae of Lindley, this one forming "a very natural group" of 4 genera, *Barringtonia* (Africa and Madagascar), *Combretodendron* (Africa), *Careya* (Indomalaysia), *Planchonia* (S.E. Asia, Australia); the genus *Foetidia*, confined to the Madagascan region, is retained in Lecythidaceae with *Napoleona* and *Crateranthus* of tropical Africa. For his part, Airy Shaw (1966) considers *Foetidia* as the type and the single member of the new family Foetidiaceae. *Foetidia* has 5 species (and several to be described), one of which is endemic to the Mascarenes and another reaching the African coast (Zanzibar). About the latter "there is no reason why it should not be native, but whether a recent arrival or a relicts of a one wider distribution is unknown," Sangai (1971) noted. *Barringtonia*, with 39 species, ranges from Africa and India to Australia; two species confined to sandy and rocky beaches, reach E. Africa and the Madagascan region.

Thus, there are two parts in this whole: a palaeotropical one with *Barringtonia* (and *Combretodendron* in Africa) and a neotropical one with *Foetidia* (distantly allied to some African genera), this one having evolved separately for a long time. Nevertheless, *Barringtonia* is to be considered in a special category as a readily dispersed mangrove genus.

Flacourtiaceae. This pantropical family of 84 genera (1,300 spp.) has 28 endemic genera in Africa sensu lato (including Madagascar and the Mascarenes) and thereby offers a special interest. It is well represented in Madagascar with 110 species and 14 genera, 8 of which are endemic (but 2 of them, *Calantica* and *Aphloia* reach E. Africa); the most evolved tribe (according to Hutchinson, 1967), Bembicieae, is endemic to Madagascar. There are 2 large pantropical genera: *Casearia* (160 sp.; 1 endemic to Madagascar and 1 to the Mascarene Islands; 11 endemic to Africa—Sleumer, 1971); *Homalium* (180 spp.; 59 spp. in Africa sensu lato, 38 of which in Madagascar, all of them endemic). Three genera are palaeotropical: *Erythrospermum* (5 spp., 2 of which endemic to Madagascar sensu lato, none in Africa); *Scolopia* (37 spp., 14 of which in Madagascar, all endemic); *Flacourtia* (60 sp.; 1, nonendemic, in Madagascar). The endemic genera are frequently pausispecific: *Prockiopsis* (1 sp.—Capuron, 1968d); *Bivinia* (2 spp.); *Bembicia* (1 sp.); *Bembiciopsis* (1 sp.); *Aphloia* (4–5 spp. or 1 polymorphic species); *Calantica* (7 spp.); except for *Tisonia* (15 spp.) and *Ludia* (23 spp.). The genus *Xylotheca* of tropical and E. Africa has 1 species in Madagascar. In the same way, *Aphloia* reaches E. Africa (Airy Shaw, 1966).

Such great a number of highly differentiated genera, that is one-third of the total number, are endemic to Africa-Madagascar that we may suppose the family to have originated there.

Violaceae (20 gen.) is represented by 3 nonendemic genera: *Viola* (1 sp., nonendemic); *Hybanthus* (75 spp., most part tropical, 4 spp. in Madagascar, 3 of which endemic); *Rinorea* (250 spp. tropical and subtropical, many African, but also well represented in South America; 27 spp. in the Madagascan region, all but one endemic).

Onagraceae (= *Oenotheraceae*) is a family of 21 genera and 640 species widespread through temperate and tropical regions, mostly as perennial herbs. There are 2 indigenous genera in Madagascar: *Epilobium* with 6 species, some of which are endemic, and *Ludwigia* with 9 species.

Turneraceae is a family of 8 genera, 6 of which are endemic to Africa-Madagascar. Two other genera also occur in this area, but are principally American: *Piriqueta* and *Turnera*. There are 3 genera in Madagascar: *Piriqueta* (3–4 endemic spp.); *Hyalocalyx*, a monotypic genus with herbaceous habit, also present in Mozambique; *Turnera* (1 nonendemic sp.). *Mathurina* (1 sp.) is a monotypic genus endemic to Rodrigues. A species attributed to *Piriqueta*, *P. integrifolia*, is an isolated taxon whose status needs to be restudied.

Passifloraceae is a family of 12 genera (600 spp.) of shrubs, vines and herbs of tropical and warm temperate regions. Two indigenous genera occur in Madagascar, *Adenia* and *Deïdamia*. The former, a palaeotropical genus of 100 species, is represented in Madagascar by 13 endemic species. The latter is an African-Madagascan genus with 6 species endemic to Madagascar and the Comores and 1 species confined to tropical Africa.

Physena. This is an isolated genus of 2 species endemic to Madagascar classified in turn in Passifloraceae, Capparidaceae, and Flacourtiaceae.

Begoniaceae. This is a small family of 5 genera particularly well represented in northern South America, but also in Pacific islands (Barkley & Golding, 1974). The genus *Begonia* with over 800 species, mostly American (Baranov & Barkley, 1974), is important in Madagascar where at least 50 species occur (Humbert, 1959).

Cucurbitaceae (116 gen., 1,200 spp.) (data according to Keraudren, 1966). This family of mainly tropical and subtropical distribution is well represented in Madagascar with 21 indigenous genera, of which 8 are endemic. Two endemic genera, *Xerosicyos* (4 spp.) and *Zygosicyos* (1–2 spp.), related to the African genus *Gerrardanthus*, are considered as primitive. The other endemic genera are: *Seyrigia* (5 spp.), related to some American genera; *Trochomeriopsis* allied to the *Seyrigia*; *Ampelosicyos* (3 spp.); *Lemurosicyos* (1 sp.); *Zombitsia* (1 sp.); and *Tricyclandra* (1 sp.). One genus, *Peponium*, is restricted chiefly to Madagascar (12 spp.) but reaches E. and S. Africa. There are 4 other African-Madagascan genera: *Oreosyce* (5 spp. in Africa, 1 sp. common to Africa and Madagascar); *Raphidiocystis* (5 spp., 1 of which special to Madagascar); *Cyclantheropsis* (3 spp., 1 of which special to Madagascar); and *Cucumella* (1 sp. in E. and S. Africa, and Madagascar). Five genera are palaeotropical: *Zehneria* with 9 Madagascan species (5 endemic); *Kedrostis* with 6 endemic Madagascan species; *Muellerargia* with 1 of its 2 species endemic to Madagascar, the other endemic to Malaysia. The American genus *Cayaponia* has some species in Africa, one of which is also in Madagascar. The pantropical (chiefly African) genus *Corallocarpus* has 3 Madagascan species, 2 of which endemic.

All of these facts support the thesis of an ancient distribution of the family in Madagascar.

Salicaceae are represented in Madagascar by 2 endemic species of *Salix*.

Capparaceae. This family of 50 genera and 800 species, primarily pantropical, has 8 genera in Madagascar, but none are endemic. Two of them, closely akin, are common to Madagascar and E. and S. Africa: *Boscia* (30 spp., 3 endemic in Madagascar) and *Thilachium* (20 spp., 9 spp. in Madagascar sensu lato, 8 endemic). The other genera are pantropical; *Crataeva* (3–4 spp. endemic to Madagascar); *Capparis* (4 spp. in Madagascar, 1–2 endemic); *Cleome* (7 spp. in Madagascar, 3 endemic); or palaeotropical: *Cadaba* (40 spp., 1 endemic in Madagascar); *Maerua* (100 spp., 5 endemic in Madagascar); *Gynandropsis* (1 adventitious sp.).

It is very surprising that this family, particularly well represented in Africa with 15 endemic genera, has no genus endemic to Madagascar. This lack of generic endemism may mean that Capparaceae reached Madagascar from Africa at a late date (about the genus *Physena*, cf. Passifloraceae).

Cruciferae (cf. Humbert, 1959).

Moringaceae (1 gen., 10 spp.). This monotypic family consists of about 10 species, 2 in India, the others in Africa-Madagascar. Aside from *Moringa oleifera*, known to be introduced, there are 2 endemic species in Madagascar, *M. hildebrandtii* and *M. drouardii*. They occur in the south and southwest of Madagascar with plants such as *Adansonia* or euphorbias and all of the genera of

Didiereaceae. In this region grow many xerophilous plants such as *Xerophyta dasylirioides*, *Selaginella nivea*, *Pachypodium* sp., *Aloe divaricata*, *Aloe suzannae*, *Rhigozum madagascariensis*, *Uncarina* sp., etc. The African species of *Moringa* are distributed in a discontinuous area in the Southwest (*M. ovalifolia*) and in the Northeast (*M. longituba*, *M. stenopetala*, *M. peregrina*). Two species are known in N. India (*M. concanensis*, *M. oleifera*) (Keraudren, 1965).

Ericaceae (*Vacciniaceae* included) (50 gen., 1,350 spp.). This is a family of cosmopolitan plants or one inhabiting mountains in the tropics. It is divided into 3 subfamilies, 1 of which, Ericoideae, is well represented in Europe and Africa, whereas the other 2 subfamilies (Vaccinioideae, Rhododendroideae) are absent or nearly so from Africa. Three genera occur in the Madagascan region: *Agauria* (7 spp.) and especially *Philippia*, with nearly 40 species, that is half of the whole genus. The widespread and very distinct genus *Vaccinium* (a special family for some authors) has only 4 Madagascan species. This genus, which occurs in S. Africa, appears absent from tropical African mountains.

According to Stevens (1970, 1971) and others, *Agauria* is closely related to the American genus *Agarista*.

Sapotaceae. Following Aubréville (1972, 1974b), the Madagascan Sapotaceae have 11 genera (85 spp., all endemics) divided into 2 subfamilies. Mimusopoideae: *Manilkara* is a pantropical genus having more than 60 species, with 7 endemic in Madagascar. Three genera are endemic: *Labramia* (8 spp.); *Fauchera* (11 spp.); and *Labourdonnaisia* (3 spp. in Madagascar, 2 spp. in the Mascarenes). *Mimusops* is a genus common to E. and S. Africa (12 spp.), the Comores (1 sp.), Madagascar (13–14 spp.), the Mascarenes (3 spp.), and the Seychelles (1 sp.) but with 1 species is widely spread over palaeotropics to the Pacific islands.

Sideroxyloideae: 3 African-Madagascan genera: *Sideroxylon*, a genus with about 15 species, well known for its disjunct distribution (Madeira, Cape Verde Islands, Teneriffe, E. Africa, Madagascar, Mascarenes); 6 species are in Madagascar and 6 species in the Mascarenes; *Donella*, 4 species in the Guineo-Congolese forest, 1 species in E. Africa, 8 species in Madagascar; *Austrogambeya*, a genus from S. Africa and Zambia, close to *Donella* and *Gambeya*, with 1 species in Madagascar. *Gambeya*, a genus principally African, with 1 species in Madagascar, but with also 1 species in S. America. Two endemic genera: *Tsebona* (1 sp.) and *Capurodendron* (22 spp.).

Judging from these data based on Aubréville's work, we must conclude that Sapotaceae appears to represent a very important and strongly differentiated Madagascan nucleus. A high degree of generic endemism, a strange disjunct distribution in Madagascar-Africa (*Sideroxylon*), an intensive differentiation of *Mimusops* species in Madagascar, many strong links with Africa where the family reaches a very high development, such are the most noteworthy aspects concerning the distributional pattern of the Madagascan Sapotaceae, from which we could infer with Raven & Axelrod (1974) that an origin in West Gondwanaland "appears most probable, almost certainly before the close of the Cretaceous."

Madagascar and its surrounding islands must have taken a considerable part

in saving from extinction many Gondwanian genera which are today morphologically and geographically isolated, such as *Sideroxylon*, *Labourdonnaisia*, and other palaeoendemics. One genus, *Northea* (5 spp.), is endemic to the Seychelles.

Ebenaceae (2 gen., 450 spp.). The pantropical *Diospyros* is represented in Madagascar by ca. 100 species, 6–7 of which occur on the African mainland or have close relatives there. The remainder are endemic to Madagascar and do not seem to be closely related to the mainland species. *Euclea* (12 spp. in Africa) has 1 species on the Comores. There are the same number of species of *Diospyros* in Madagascar as in tropical Africa, and ca. 80 species in tropical America. About 250 species are currently accepted from tropical Asia, but this figure must be much too high (F. White, personal communication). Although he has not yet given any serious thought to the place of origin of the family, White inclines to the belief that it might have been the African part of Gondwanaland (White, pers. comm.).

Myrsinaceae (35 gen., 1,000 spp.). This family is a very natural one whose 7 genera occur in Madagascar: 2 pantropical: *Rapanea* (190 spp., 1 in the Seychelles, 1 in Madagascar, 2 in the Comores) and *Ardisia* (2 spp. in Madagascar, 2 spp. in the Macarene); 2 palaeotropical: *Embelia* (100 spp. in 8 subgen., 2 of which in Madagascar containing 8 spp.) and *Myrsine* (7 spp. in China, India, Africa, Azores; 1 endemic sp. in Madagascar); 3 endemics: *Monoporus* (8 spp. from sea coast to mountains), *Oncostemon* (97 spp. in Madagascar, 3 in the Comores, 3 in Mauritius), *Badula* (14 spp. in the Madagascan region: 3 in Madagascar, 3 in the Réunion, 7 in Mauritius, 1 in Rodriguez).

It is interesting to note that the pantropical genus *Ardisia* is represented in Madagascar by a subgenus endemic (*Madardisia*) and in Africa by another subgenus (*Afrardisia*). These facts seem to at least prove some antiquity of the genus in Africa-Madagascar.

Madagascar must have been a part of the ancient continent where Myrsinaceae originated. Let us note in passing an unusual intense speciation in the genus *Oncostemon*.

Primulaceae (cf. Humbert, 1959).

V

Cunoniaceae. This typically austral family (27 gen., 260 spp.) is represented in Madagascar by only the genus *Weinmannia* and over 20 species. This genus with 150 species ranges from the Philippines and New Caledonia to tropical America, where it is particularly abundant, but it is absent from Africa, India, and Australia. There are 2 genera of Cunoniaceae in S. Africa: *Cunonia* (about 15 spp. in the Malay Archipelago and New Caledonia, 1 endemic species in S. Africa); and *Platylophus*, the latter being monotypic and endemic. All of the Madagascan species, which Bernardi (1965) has divided into 4 sections, are endemics.

In spite of its scanty representation in the Madagascan region (Madagascar and S. Africa), the family Cunoniaceae provides some most valuable facts. First, there is one and only one endemic genus, and this one is monotypic: a fact

whose significance is obvious: the genus *Platylophus* testifies in favor of S. Africa as a center of survival for Gondwanaland inhabitants. Second, the link between S. Africa and Madagascar is not less obvious. Third, the genus *Weinmannia* has been subjected to very active speciation since Madagascar separated from Africa. The lack of fossils prevents a definite statement about its possible presence in Africa in the past.

Pittosporaceae. This typically palaeotropical family of 9 genera, 8 of which are endemic to Australasia, is represented in tropical Africa sensu lato by the genus *Pittosporum* which contains over 150 species, spread from Hawaii to the Canary Islands. There are perhaps 25 species in tropical Africa, 10 of which are in Madagascar; all of them, but 1, endemics.

This family offers a remarkable case of biogeographical meaning. The distribution pattern of the genus *Pittosporum* (Cufodontis, 1960), if regarded as an isolated genus, is almost meaningless, but in relation with the whole of its family, it becomes probable that its distribution center must have been Australasia, perhaps in the Upper Cretaceous or later when Australia and Africa were still in close proximity. However, the relationships of the family being somewhat problematic, it is difficult to know for certain where it originated.

Crassulaceae. This is a family of wide, cosmopolitan distribution consisting of 35 genera and 1,500 species, often growing in dry regions, chiefly in S. Africa and the Mediterranean region, but also in Asia and Central America. It is represented in Madagascar by 3 genera: *Crassula* (5 ssp. all of them endemic), *Sedum* (1 sp., endemic) and *Kalanchoë* (57 spp. of which 55 endemic). There is no endemic genus. Affinities are strongly African (P. Boiteau, pers. comm.).

Saxifragaceae. For want of being revised this family proved difficult to interpret. Many genera formerly included in it (*Brexia*, *Roussea*, *Forgesia*, *Grevea*, *Montinia*) are now either incorporated with Escalloniaceae (Hutchinson) or distributed among small new families. Given our present knowledge, the latter alternative seems the best one.

Brexiaceae is a small family of 2–3 genera with only a few species: *Brexia* in Madagascar and the Seychelles (1–2 spp., 1 of which is also in E. Africa); *Roussea* (1 sp. in the Mascarene); *Ixerba*, the affinities of which are uncertain, in New Zealand.

Montiniaceae is a family of tropical Africa and South Africa consisting of two very distinct genera (each of them should be raised to the subfamily level): *Montinia* (1 sp. in South Africa) and *Grevea* (3 spp., one of which reaches the western parts of Madagascar). The recently discovered *Grevea bosseri* Letouzey by P. Sita in Zaïre (Letouzey, 1977a) confirms Africa as probable center of origin for Montiniaceae and extends the area of the remarkable genus *Grevea*. It is noteworthy that *Grevea madagascariensis* is present on Madagascar, as, conversely, *Brexia madagascariens*is is on the African coast: the Mozambique canal has been a poor gap between Africa and Madagascar.

Escalloniaceae. Following Airy Shaw (1966), I maintain, at least provisionally, the genus *Forgesia* in this ill-defined family. This genus is monotypic and endemic to the Mascarene Islands.

Rosaceae is a family of wide distribution which contains 124 genera and over

3,300 species. It is represented in Madagascar by only 6 indigenous genera, one of which, *Grangeria*, is endemic. Besides the genus *Rubus*, they belong in two tribes: first, *Pygeum* (3 spp., 1 endemic), second, *Parinari* (a pantropical genus with 2 spp. endemic to Madagascar), *Licania* (a large austral genus with 1 Madagascan nonendemic sp.), *Hirtella* (another large austral genus, with 4 sp. endemic to Madagascar, 2 of which described by Capuron, 1972b), *Grangeria* (a monotypic and endemic genus).

Although very poorly represented, the family Rosaceae is interesting in that its links with Africa, are well marked by the genera *Hirtella* and *Grangeria*, which belong in one and the same tribe.

Leguminosae (*Caesalpiniaceae*, *Mimosaceae*, *Papilionaceae*). The revision of the Madagascar Leguminosae by M. Peltier is in progress but still far from complete. So, it is impossible to form an accurate opinion about Madagascan elements. In referring to work by Capuron (1967a, 1968b, 1970b), Viguier (1944), and Peltier (pers. comm.), there would be approximately 98 genera and 600 species. Since the Humbert's (1959) essay, Capuron (1967a) has described 2 new genera of Caesalpinioideae: *Elignocarpus* and *Mendoravia*, bringing the number of endemic genera to 11 out of 25. This is a very strong generic endemism. And this fact concerning the most primitive subfamily seems all the more important as the number of endemic genera is proportionally inferior in Papilionoideae and reduced to one in Mimosoideae. At the specific level, endemism is about 50% in Papilionioideae, 70–75% in both of the other subfamilies. One genus, *Bremontiera* (1 sp.), is endemic to the Mascarenes.

Podostemaceae (40 gen., 200 spp.) (according to C. Cusset, 1974, oral comm.). This family taken sensu stricto is represented in Madagascar by 4 genera, only 1 of which nonendemic: *Sphaerothylax* (3 spp.: 1 confined to Cameroon; 1 to S. Africa, reaching Angola and Zambia; 1 in E. Africa, Ethiopia and Madagascar). The 3 endemic genera are: *Thelethylax* (2 spp. endemic), closely allied to *Ledermanniella*, an African genus of 47 species, particularly abundant in Cameroon-Gabon; *Endocaulos*; and *Palaeodicraeia*. These last 2 genera are morphologically noteworthy with their deciduous leaves, the blade falling off and the persistant sheath becoming thick. This character unknown in African Podostemaceae exists in Asia (*Hydrobryum*, *Zeylanidium*). With respect to other characters, affinities are likewise with Asia. There is no link with the American element (C. Cusset, pers. comm.).

Tristichaceae, a family often merged into Podostemaceae, consists of 4–5 genera: 1 in Amazonia, 2 in Asia, 1 pantropical (with several spp., of which 1, *Tristicha trifaria*, in Madagascar and S. Africa; another, *T. alternifolia* in Madagascar and Africa [and America?]; 1, *T. hypnoides* in South and Central America; 1 in Australia—possibly a new genus) (C. Cusset, pers. comm.).

This distributional pattern, with 3 endemic genera in Madagascar, seems to indicate that the Podostemaceae could have had a Gondwanian origin by the close of the Cretaceous times.

Haloragaceae (6 gen., 120 spp.) (cf. Humbert, 1959).

Lythraceae. A family of herbs (often hygrophilous) and shrubs widespread throughout the World containing 25 genera and 550 species. It has 6 indigenous

genera in Madagascar, one of which is endemic, and 20 species, half of which are endemic. One genus, *Tetrataxis* (1 sp.), is endemic to the Mascarenes.

No clear meaning is to be drawn from the presence in Madagascar of widespread genera such as *Nesaea*, *Rotala*, *Ammania*, whose 10 or so species are nevertheless endemic to Madagascar. In contrast, we have to focus interest on *Woodfordia* and *Pemphis* which are small palaeotropical genera, each of them consisting of 2 species: *Woodfordia* with 1 African species and a widespread one ranging from Africa and Madagascar to Indonesia; *Pemphis* with 1 species, littoral, reaching the Pacific Islands, and the other endemic to Madagascar. Moreover, a monotypic genus, endemic to Madagascar, *Capuronia*, was described by Lourteig (1960); it is the single dioecious Lythraceae.

Sonneratiaceae. This small family of 2 genera and 7 species is of special interest in that it is centered in South Asia, although the mangrove genus *Sonneratia* reaches the African coast with one species. But this very distribution provides evidence in favor of links between the Madagascan region (including E. Africa) and E. Asia, to the exclusion of the West African coast. It is one of the characteristic elements of the floristic oriental belt.

Thymelaeaceae (*Aquilarioideae* included) (50 gen., 600 spp.). Mainly in temperate regions (Mediterranean region, S. Africa, Australia . . .), this family is very akin to the families Penaeaceae (5 gen.) and Geissolomataceae both of of them endemic to S. Africa. There are 7 genera in Madagascar, 2 of which palaeotropical (*Lasiosiphon*, *Gnidia*). Four genera are common to Madagascar and Africa: *Peddiea*, 1 endemic species in Madagascar; *Synaptolepis*, 1 endemic species in Madagascar; *Dais*, 1 endemic species in Madagascar, 1 species in S. Africa; *Octolepis*, 3 species, morphologically isolated and primitive (with a perianth deprived of tube), represented in Madagascar by 1 species (which will have to be raised at the subgeneric level), which is dioecious and endemic. One genus, *Stephanodaphne*, is composed of 9 species, 1 of which is endemic in the Comores.

The family, therefore, is strongly attached to Africa. According to Léandri (1947) the genus *Synaptolepis* is related to the American genus *Lophostoma*. The family is an heterogenous assemblage divided into several phyla, in particular the *Synaptolepis* one, the *Stephanodaphne* one, the *Peddiea* one.

Myrtaceae (100 gen., 3,000 spp.). This is a family mainly developed in Australia and tropical America, but with a monotypic, endemic subfamily (Heteropixioideae) in S. and S.E. Africa. There are 3 indigenous genera in Madagascar: *Myrtus* with 2 endemic species, *Eugenia* (35 spp.), and *Syzygium* (20 spp.). Many species also occur in the Mascarenes and Seychelles, and one monotypic family, possibly related to the Myrtaceae, the Psiloxylaceae, is endemic to the Mascarenes.

Melastomataceae (250 gen., 4,000 spp.). The Madagascan Melastomataceae being in badly need of revision, it is not possible to have any clear view about their composition and affinities. According to Perrier de la Bâthie (1951), there are 10 indigenous genera, 5 of which endemic. Since then, the genus *Rousseauxia* has been restated (Jacques-Félix, 1973) and the geographical distribution of two genera given as Madagascan has been altered.

In any case, there are 4 genera endemic to Madagascar-Mascarenes: *Rhodosepala* (1 sp.), *Dionycha* (3 spp.), *Amphorocalyx* (5 spp.), and *Rousseauxia* (13 spp.), and 5 common to Africa: *Gravesia* (100 spp. in Madagascar, 7 sp. reaching E. Africa and some spp. in tropical Africa), *Dichaetanthera* (20 spp. in Madagascar, 1 endemic to Africa), *Tristemma* (15 spp.), *Anthostemma* (1 sp. in Africa, 1 in Madagascar), *Dissotis* (2 African spp.). The other two genera are palaeotropical: *Medinilla* (70 spp. in Madagascar) and *Memecylon* (56 spp. in Madagascar).

Combretaceae. As stated by Exell (1972) and Exell & Stace (1966), this family is composed of 19 genera (475 spp.): 13 in Africa-Madagascar, with 7 endemic, 3 palaeotropical, 2 widespread, 8 in Asia with 2 endemic, 8 in America with 4 endemic, 3 in Australia with 1 endemic. There are overall 14 genera endemic to any region, 2 widespread genera, and 3 mangrove genera, and the family is centered in Africa (Liben, 1971). There are 62 species in 5 genera in Madagascar (Capuron, 1973a), 2 of which have a pantropical distribution: *Terminalia* (50 spp. in Malaysia, 35 in Madagascar, 30 in Africa, 30 in America, only some in Australia) and *Combretum* (100 spp. in Africa, 35 in America, 35 in Asia, and only 4 in Madagascar). *Meiostemon* is an African-Madagascan genus of 2 species: 1 species is endemic to Madagascar, and 1 species is endemic to the Sudano-Zambezian area. The endemic genus *Calopyxis*, which is characterized by lacking petals and by the corollalike structure of its receptacle, has as many species as 22, which is a very high number proportionally to the area. Madagascar, like Amazonia, and the Malaysian Islands, is a center of strong speciation (Exell & Stace, 1966).

Some facts must be noted. First, the active speciation of 2 genera (*Terminalia*, *Calopyxis*) might have started after Madagascar separated from Africa. One can add that *Lumnitzera*, the fifth genus in Madagascar (1 mangrove sp.), is a strictly palaeotropical genus. All of tribes and subtribes are represented in, one of which (*Pteleopsidineae*) is endemic to, the African-Madagascan area. A subfamily, Strephonematoideae (raised by some authors—Venkateswarlu & Rao, 1971—to familial level) containing 7 species, is endemic to Africa.

Proteaceae (75 gen., 1,000 spp. according to Johnson & Briggs, 1975). This family is mainly of southern tropical distribution with two major centers: Australia (45 gen. with 35 endemic) and South Africa (14 gen.). However, some genera reach Central America, Ethiopia and China. Johnson and Briggs have divided the family into 5 subfamilies, 2 of which are present in Madagascar: Proteoideae (1 tribe, Conospermeae, out of 3) and Grevilleoideae (1 tribe, Macadamieae, out of 7). All of the 14 South African genera, 2 of which (*Faurea*, *Protea*) extend far northward, belong to the Proteoideae.

There are 3 genera in Madagascar with 2 endemic. The monotypic genus *Dilobeia* stands apart and represents a subtribe of its own (Conospermeae—Dilobeiinae). *Faurea* (18 spp.), a tropical African genus classified in the Conospermeae—Proteinae, has one species in Madagascar. The third genus, *Malagasia*, with only one species, is the only representative of the subtribe Hicksbeachiinae (Macadamieae) in the African region; its closer ally in the same tribe could be *Heliciopsis* the sole genus endemic to Asia to the west of

Wallace's Line. It is noteworthy that another monotypic and isolated genus in the Macadamieae, *Brabeium*, inhabits S. Africa.

The Madagascan Proteaceae (besides *Faurea*) are obviously some rare relicts of a continuous ancient southern area. Johnson and Briggs think that the family could have originated in Gondwanaland in the Albian at the latest.

Rhizophoraceae. This family (160 spp.), which includes 18 genera, is basically palaeotropical. In the Madagascan-African area one finds 9 genera, 4 of which are endemic: *Anopyxis* (3 spp.), *Macarisia*, *Comiphyton* (1 sp.) (Macarisiae—Floret, 1974), and *Poga* (1 sp.) (Anisophylleae). All of the tribes are represented in this area, and the Macarisieae, which reaches America (*Sterigmapetalum*, an endemic genus of 3 spp.) and India (*Blepharistemma*, a monotypic and endemic genus) has its principal center of differentiation here (Floret, 1976).

There are 7 genera in Madagascar (22 spp. with 17 endemic): 3 mangrove genera (Rhizophoreae): *Ceriops*, a genus with 2 species, palaeotropical, 1 of which, *C. tagal*, reaches E. Africa, Madagascar, and the Seychelles; *Bruguiera*, with 6 species, palaeotropical, 1 of which, *B. gymnorrhiza* also reaches E. Africa, the Seychelles, and Madagascar; *Rhizophora*, a genus of 7 tropical species, 1 of which, palaeotropical, *R. mucronata*, occurs in E. Africa, Madagascar, the Seychelles, and the Mascarenes. The palaeotropical genus *Carallia* (Gynotrocheae) has 10 species of which *C. brachiata*, reaches the Madagascan rain forests. The other 3 genera are *Macarisia* and *Cassipourea* (Macarisieae) and *Anisophyllea* (1 endemic sp.) (Anisophylleae). The tribe Macarisieae is strongly rooted on Madagascar with the endemic genus *Macarisia* (2 spp.) and *Cassipourea*, a large genus reaching S. India and S. America, with 10 species endemic to Madagascar.

The family has only 2 genera endemic to America: *Polygonanthus* (Anisophylleae) and *Sterigmapetalum*.

From this distribution, one may suppose that the differentiation of the family might have begun by the time when America and Africa started separating so that a small part of the first members of it were trapped in America. Africa-Madagascar-India might have been the principal primary center of taxogenesis later in the Cretaceous. In any way, the family is obviously centered around the India Ocean.

Concerning the position of the Rhizophoraceae in the Myrtales, the recent work on wood anatomy by van Vliet (1976) suggests the family does not belong to this order, but rather to Cornales (following the Thorne's [1968] classification).

Alangiaceae. This monotypic family which has for a long time been included in Cornaceae covers a typically oriental area: Vietnam (7 spp.), China (6 spp.), Sumatra (8 spp.), Borneo (8 spp.), Java (7 spp.), Japan (2 spp.), E. Australia (1 sp.), New Caledonia (1 sp.). However, the genus *Alangium* is also represented in the African-Madagascan area by 3 very distinct species, one of which, *A. griselleoides* Capuron, is endemic in Madagascar. Judging from the incomplete material at his disposal, Capuron (1962) suggested wrongly that it could belong to section *Conostigma*. In all certainty, the Madagascan species is to be placed with *A. chinense* and *A. barbatum* in section *Marlea* Baill. close to

section *Angolum* Baill. to which belongs *A. salviifolium*. The present Indo-Malesiano-Australian area displays one African-Madagascan branch with 3 species. Besides, it is notable that the Madagascan species is dioecious and is the single one within the genus to be so. In all probability, this advanced character must have been acquired after Madagascar separated from Africa, possibly recently. Moreover, the Madagascan species, unlike the species of *Conostigma*, does not have a primitive secondary xylem with scalariform perforation plates (Eyde, 1972).

The fossil material of Alangiaceae, *Alangioxylon*, *Alangiopollis* (Reitsma, 1970), at our disposal shows that the distribution of the family reached Europe and N. America during Eocene-Miocene times. For Reitsma, *Alangiopollis eocaenicus* Krutzch (Germany, London Clay Flora) could be considered to be one of the ancestors of the family and, though referring only to pollen, he thinks *A. griselleoides* might represent the end product of a line coming from this fossil taxon through *A. barbatum*. The placement of *A. griselleoides* in *Marlea* supports this hypothesis.

I agree with Aubréville (1976b) that this member of the Madagascan flora belongs to a Laurasian line. It might have reached Madagascar in the late Eocene when the Thethys became interrupted, permitting connections between Africa and the northern continents.

Cornaceae. It is not certain that this family occurs in Madagascar, the two Madagascan genera formerly attributed to it being now considered to constitute a special endemic family Melanophyllaceae (Airy Shaw, 1972). It is even possible that this one will have once again to be divided as the morphological gap between the two genera appears substantial. *Melanophylla* has 9 species, *Kaliphora* only one.

Olacaceae is a tropical family (24 gen., 230 spp.) that has 4 genera in Madagascar, of which 1 is endemic with 3 species: *Phanerodiscus*. There is 1 pantropical genus, *Ximenia*, with 3 species out of 12 over the World, with 2 endemic, and 1 common to Madagascar and Africa. There are 2 palaeotropical genera: *Olax* (50 spp.) with 7 species in Madagascar and the Mascarene Islands of which 6 are endemic and 1 is common to Madagascar and Africa; *Anacolosa* (16 spp.) with 2 species in Madagascar (Capuron, 1968a).

Opiliaceae is a palaeotropical family of 8 genera of which 1, *Rhopalopilia*, is endemic to Madagascar-tropical Africa: 5 species are endemic to Africa, 2 are endemic to Madagascar, and 1 is common to Madagascar and Africa (Capuron, 1968a).

Santalaceae, *Loranthaceae* (cf. Humbert, 1959).

Balanophoraceae (18 gen., 45 spp.). This family of parasitic plants has 3 genera in Madagascar, 5 in Africa, 1 of which, *Balanophora*, is a palaeotropical genus that occurs in Madagascar and W. Africa. One Madagascan genus, *Ditepalanthus*, is endemic and monotypic, the third is *Langsdorffia*, a genus classically known as confined to America, but present also in New Guinea (Hansen, unpublished paper 1976). *Langsdorffia malagasica* (= *Thonningia malagasica*) is a dioecious parasite on roots of *Elaeocarpus quadrilobus*, an austral genus absent from Africa.

What is of particular interest is that 5 genera are endemic to Madagascar-Africa, distributed in 4 subfamilies of which 2 endemic. *Mystropetalon* (1–2 spp.) is endemic to S. Africa (according to Airy Shaw, 1966, this genus should be given family rank). The Sarcophytoideae is composed of 2 genera: *Sarcophyte* (2 spp. in E. Africa and Transvaal) and *Chlamydophyton* (equatorial West Africa). The subfamily Balanophoroideae has 2 genera in Africa: *Balanophora* and *Thonningia*, an endemic genus. The Helosioideae, in which the Madagascan *Ditepalanthus* is placed, is absent from Africa but has 3 endemic genera in America (*Scybalium*, *Helosis*, *Corynaea*) and 3 others in Asia. *Ditepalanthus* is related to *Rhopalocnemis* (Himalaya, Vietnam, Indonesia) (Hansen, unpublished paper, 1976).

It is to be noted that *Langsdorffia malagasica* and *Ditepalanthus* are landmarks between America and Palaeotropics.

The distributional pattern of the Balanophoraceae is typically austral and supports the idea that the family must have had a Gondwanian origin.

Hydnoraceae (2 gen., 20 spp.). This is a very interesting bitypic family of parasites of the Southern Hemisphere restricted to the Madagascan region sensu lato and America. *Hydnora* is composed of about 10 species, one of which is endemic to Madagascar and represents a section of its own, *Neohydnora*; the other species inhabit in S. and E. Africa. The other genus *Prosopanche* is endemic to S. America (Paraguay, Argentina).

The placing Hydnoraceae (Rafflesiales) near Santalales is of special interest because the Balanophoraceae-Hydnoraceae is a biogeographically homogenous unit.

Rafflesiaceae (8 gen., 50 spp.). There are 3 endemic species of *Cytinus* in Madagascar, a genus confined to Africa and W. Europe.

Celastraceae (*Hippocrateoideae* excluded). This is a family of tropical and temperate plants dispersed all over the world, although more abundantly in S. America, and contains 60–90 genera (800–1,000 spp.). According to Lobreau-Callen's (1975) work, it is, with the Icacinaceae and several small families, a member of an austral complex. It is of special interest with respect to Madagascar where at least 14 genera occur (4 of them being still undescribed), 10 of which are endemic: *Polycardia*, 9 species; *Ptelidium*, 2 species; *Hartogiopsis*, 1 species; *Salvadoropsis*, some species; *Brexiella*, 2 species; *Evonymopsis*, 4 species. The other genera are widespread (*Celastrus*) or pantropical (*Elaeodendron*, *Maytenus*), or African-Madagascan (*Mystroxylon*).

So generic endemism is extraordinarily high, a proportion of 2:3. But this interpretation is only a provisional account as the family is in badly need of revision. One monotypic genus (*Herrya*) is endemic to Réunion.

Hippocrateoideae (N. Hallé, unpublished paper) (24 gen., 320 spp.). This subfamily is mainly developed in Africa-Madagascar with 17 genera, 9 of them endemic, and 150 species. There are only 6 genera (11 sp.) with none endemic in Madagascar: *Apodostigma* (1–2 spp. common to Madagascar and Africa); *Reissantia* (1 sp. in Madagascar, 4 spp. in Africa, 3 spp. in Asia-Melanesia); *Loeseneriella* (2 spp. in Madagascar, 12 ? spp. in Africa; 8 ? spp. in Asia-Melanesia); *Elachyptera* (1 sp. in Madagascar, 3 spp. in Africa, 3 spp. in America); *Pristimera* (4 spp.

in Madagascar, 5 spp. in Africa, 9 spp. in America); *Salacia* (2 spp. in Madagascar, 90 spp. in Africa, 30 spp. in Asia-Melanesia, 29 spp. in America).

Salvadoraceae, *Aquifoliaceae* (cf. Humbert, 1959).

Icacinaceae is a family of pantropical distribution with 58 genera and 400 species. It is represented in Madagascar by 8 genera, of which 4 Madagascan-African (*Cassinopsis*, 4 endemic spp., 2 spp. endemic to S. Africa; *Leptaulus*, 1 endemic Madagascan species, 2 species endemic to tropical Africa; *Desmostachys*, 1 species in Madagascar, Comores, S. Africa, 2 species endemic to Africa; *Raphiostyles*, 6–7 species in Africa, 1 species endemic to Madagascar; 3 palaeotropical (*Apodites*, *Iodes*, *Pyrenacantha*); 1 endemic, *Grisollea*, which contains 2 species, of which 1 is restricted to the Seychelles.

Dichapetalaceae is a small family (3 gen., near 100 spp.) nearly confined to the tropics. It is represented in Madagascar by 14 species, all of them endemic, belonging to genus *Dichapetalum*, a pantropical one that is by far the largest in the family, and which is abundantly present in Africa (⅔ of the whole—Breteler, 1969).

Buxaceae (5 gen., 50 spp.). The plants of this family occur mainly in temperate regions of the northern hemisphere, but also in tropical mountains. The family reaches the southern hemisphere with 2 genera: *Styloceras* (tropical S. America, perhaps a special family) and *Buxus* sensu lato. The latter is present in Madagascar with an isolated group of 2 species, *B. madagascarica* and *B. macrocarpa*, which is strongly related to species of E. and S. Africa.

Euphorbiaceae (300 gen., 7,500 spp.). This is a family of almost cosmopolitan distribution, mainly of the tropics, with two large centers of distribution: tropical America and Africa. The new taxonomic results that have been obtained for Madagascan Euphorbiaceae during the last twenty years, part of which are not yet published, provide some new insights (Léandri, oral comm.). In particular, we must cite the Webster's (1975) work, which has modified the former systematics and suggests new ways of approaching origins and affinities. Following this author, there would be 5 subfamilies in Madagascar: Phyllanthoideae (7 tribes), Oldfieldioideae (1 tribe), Acalyphoideae (16 tribes), Crotonoideae (7 tribes), Euphorbioideae (3 tribes). Thus, 34 (out of a whole of 52) tribes are present in Madagascar. Thanks in particular to Capuron, the number of Madagascan genera amounts now to 62, 14 of which are endemic. There are about 600 species, of which nearly 540 are endemic (J. Léandri, oral comm.).

Special mention must be made of the genera *Voatamalo* (2 spp., endemic to Madagascar) and *Androstachys* which are related to one another and represent a very singular group (Androstachyaceae Airy Shaw). *Androstachys* has several species in Madagascar, one of which (a kind slightly different) is also present in E. Africa. One monotypic genus, *Cordemoya*, is endemic to the Mascarenes.

This family is well represented in Madagascar, but its revision is not advanced enough to permit taxogenetic or biogeographical conclusions.

Rhamnaceae. This is a cosmopolitan family of 50 genera and 600 species which is represented in Madagascar by 10 genera and 22 species (Capuron, 1965a, 1966a). Four genera are pantropical: *Colubrina* (12 spp., 5 in Madagascar

with 1 endemic); *Guania* (60 spp., 5 in Madagascar with 3 endemic); *Scutia* (7–8 spp., 1 common to Madagascar, the Mascarenes, India, S. and E. Africa); *Ziziphus* (40 spp., 3 in Madagascar with 1 endemic). Two genera are palaeotropical: *Helinum* (3 spp., 1 in both Madagascar and S. and E. Africa); *Ventilago* (25 spp., 1 common to Madagascar and India). Three genera are common to Africa and Madagascar: *Lasiodiscus* (9 spp., 2 of which are endemic to Madagascar-Comores); *Phylica* (60 spp. in S. and tropical Africa, 1 in Mascarenes, 1 in Madagascar, both endemics); *Berchemia* (22 spp., 1 of which in Madagascar, endemic). The 1 endemic genus is *Bathiorhamnus* (3 spp.).

It is remarkable that the genera are relatively numerous but the species few, one genus, and 11 species (50%) only being endemics. Only one genus (*Bathiorhamnus*) is really Madagascan, the others (pantropical, Asian or African), it seems, have come there accidentally.

Leeaceae is a palaeotropical monogeneric family of 80 species with 2 species in Madagascar: one of which endemic, the other being African-Madagascan (Descoings, 1967).

Vitaceae. This family of about 12 genera and over 800 species, which ranges throughout tropical and warm temperate regions, is represented in Madagascar by 51 species belonging to 5 genera: 3 large pantropical ones (*Ampelocissus*, *Cyphostemma*, *Cissus*) with 47 species in all of them and but 1 of these species endemic; 1 palaeotropical (*Cayratia*) with 3 endemic species; 1 (*Rhoicissus*) with 10 species, primarily of E. Africa, but 1 of them reaching the Comores. There are no endemic genera (Descoings, 1967).

Connaraceae. This family of 25 genera and 200 species is of a particular interest because it principally covers a palaeotropical area and its main center of distribution is the African-Madagascan area where 16 genera occur, 11 of which are endemic. It is, however, poorly represented in Madagascar where only 5 genera occur, none being endemic. Some aspects, however, call for special mention: 1 African genus, *Byrsocarpus*, occurs there with 1 endemic species and 1 species common to Africa. There are 3 palaeotropical genera: *Ellipanthus* (1 sp.), *Agelaea* (3 spp.), *Cnestis* (4 spp.), and a pantropical one, *Rourea* = *Santaloides* (2 spp.). All of the Madagascan species are endemic.

Sapindaceae. This tropical and subtropical family is composed of woody plants which number 2,000 species distributed in 150 genera, 28 of which, with 89 species, are present in Madagascar, the Comores, and the Mascarenes (Capuron, 1969). Nine genera are endemic (*Conchopetalum*, 2 spp.; *Plagioscyphus*, 10 spp.; *Tsingya*, 1 sp.; *Beguea*, 1 sp.; *Chouxia*, 1 sp.; *Tinopsis*, 10 sp.; *Pseudopteris*, 2 spp.; *Tina*, 6 spp., *Neotina*, 2 spp.); *Doratoxylon* with 5 species occurs in the Mascarenes; *Hornea* with 1 species is endemic to the Mascarenes; *Molinea* with 6 species has 3 of them in the Mascarenes. One genus, *Stadmannia*, reaches the Mascarenes and E. Africa. Three genera are common to Madagascar and E. Africa: *Erytrophysa*, *Macphersonia*, and *Camptolepis*. Five genera are widespread in Africa: *Zanha*, *Majidea*, *Deinbollia*, *Crossonephelis*, *Haplocoelum*. Two genera are palaeotropical: *Filicium*, *Aphania*. Three genera are pantropical: *Allophylus*, *Dodonea*, *Cardiospermum*. One genus which is mostly

American, but also occurs in Africa, has 1 nonendemic species in Madagascar: *Paullinia pinnata* (probably recently introduced). Endemic to the Madagascan region are 79 species, and 4 species are endemic to Madagascar-E. Africa. It must be noted that the pantropical genus *Dodonaea*, highly developed in Australia, has a species endemic to Madagascar, *D. madagascariensis*. *Cossinia* (4 spp.) is only found in New Caledonia and Madagascar (Good, 1950).

The Madagascan Sapindaceae of which a detailed analysis on a biogeographical basis remains to be done seem to have no direct link with the American flora.

Burseraceae. This is a tropical, woody family of 20 genera and 550 species which is represented in Madagascar by 4 genera: *Canarium* (a palaeotropical genus of 100 spp.) with 2–3 endemic (?) species. *Protium* (a pantropical genus of 85 spp., mostly in tropical America) with 1 species in Mauritius and 1 species in Madagascar, these 2 species constituting a special section (Capuron, 1968c). *Commiphora* and *Boswellia*, with more than 200 species, are endemic to Africa and Madagascar occurring in arid or rather dry regions, particularly in northeastern Africa. There are more than 40 species of *Commiphora* in Madagascar, and only 1 of *Boswellia*: *B. madagascariensis* Capuron. This species must be considered as the type of a remarkable subgenus derived from African stock: it has unisexual flowers and valvate petals (besides, its stigma is sessile). The Madagascan Burseraceae are strongly linked to the African flora.

Anacardiaceae is a chiefly tropical family of 600 species distributed in 60 genera. It is represented in Madagascar by 9 indigenous genera, of which 3 are endemic: *Operculicarya* (3 spp.), *Faguetia* (1 sp.), *Micronychia* (5 spp.). There are 2 African-Madagascan genera: *Protorhus*, 16 species with only 1 outside Madagascar and endemic to South West Africa; *Sorindeia*, 1 species endemic to Madagascar, 1 Madagascan-African species. The other genera are: *Gluta*, 1 endemic species, 12 Indomalesian species; *Campnosperma*, 15 tropical species; *Poupartia*, 5 Madagascan species, 7 in Africa, 1 in India. *Poupartia caffra* is with *Maytenus* sp. a characteristic element of African-Madagascan savannas.

Simaroubaceae (30 gen., 200 spp.). This is a family of a special interest in the Madagascan region, with 5 genera, 2 of which are endemic. A closely related (if distinct) family, Ptaeroxylaceae, also occurs in Madagascar with 1 genus, while the other genus occurs in South Africa. The main center of distribution of Simaroubaceae is in tropical America, but there is a secondary center in West Africa (Nooteboom, 1962). The Madagascan genera are: *Perriera*, 2 endemic species; *Pleiokirkia*, 1 endemic species. The other 3 genera are represented each by one species: *Quassia indica*, *Suriana maritima* and, in the Seychelles, *Soulamea terminalioides*, an endemic species. This is a surprising distribution as *Soulamea* has 6 species endemic to New Caledonia, 1 in Fiji, whereas another ranges from Polynesia westwards to Borneo. As noted by Nooteboom "*Suriana* and *Soulamea*, both belong to the *Barringtonia* formation. The fruits are certainly dispersed by seawater and this seems to have been very effective." *Quassia indica* is a palaeotropical species dispersed throughout Asia to Australia.

The Madagascan Simaroubaceae have no link with America, a meaningless link with Asia, but a strong link to the African center.

Ptaeroxylaceae (2 gen., ca 4–5 spp.). This family, possibly a subfamily of Simaroubaceae, is special to the Madagascan region sensu lato: *Ptaeroxylon* is a monotypic genus endemic to E. and S. Africa. *Cedrelopsis* (3–4 spp.) is endemic to Madagascar (Leroy, 1959).

Rutaceae. This large family (150 gen., 1,000 spp.) is rather poorly represented in Madagascar and the Mascarenes with 9 indigenous genera, of which only 1 is endemic, and 65 species, but it offers some patterns of distribution of great interest. Since 1950, owing to Capuron's (1967b) work, our knowledge about the Madagascan Rutaceae has much advanced. In particular, he found 3 genera new for the Madagascan flora, 1 of which, *Evodia*, is endemic and contains 10 species. The remarkable genus *Chloroxylon*, considered until now as Asian, and monotypic, is present in Madagascar with 2 endemic species (Capuron, 1961). Thus, the subfamily Flindersioideae, composed of both *Chloroxylon* and the New Caledonian genus *Flindersia*, extends to Madagascar. This is a distribution that seems strongly relict and suggests the possibility of the existence of direct migration between Madagascar and New Caledonia via India, possibly through rafting.

Toddalieae is represented not only by a meaningless species of *Toddalia*, but also by the genus *Fagaropsis*, which contains 5 species: 3 in tropical Africa and 2 in Madagascar. It is closely related to the Asian *Phellodendron* and this pattern of distribution is to be classified with the precedent one (Capuron, 1961).

Regarding the Xanthoxyleae, we have to put aside the pantropical genus *Xanthoxylum*, although it is present in Madagascar with 8 endemic species. The remaining genera, *Evodia* and *Ivodea* have an interesting distribution. The large palaeotropical *Evodia* (130 spp.), which is absent from Africa, has 19 endemic species in Madagascar, and *Ivodea* is a Madagascan endemic (Capuron, 1961). This pattern of distribution is comparable to other two reported above.

The remainder, *Vepris* (40 spp.), *Diphasia* (5 spp.), and *Teclea* 25 spp.) represent a very natural group nearly confined to Madagascar-Africa, except for 1 *Vepris* species that extends to India. This genus is particularly well represented in Madagascar and the Mascarenes with some 30 species, while *Teclea* has only 1 species in Madagascar. *Diphasia* consists of 2 species, 1 African, 1 Madagascan.

Meliaceae (51 gen., 550 spp.—Leroy, 1977c). This is a pantropical family of woody plants divided into 5 subfamilies, all of them represented in Madagascar, and 3 of them monotypic and restricted to the "Grande Ile": Quivisianthoideae, Capuronianthoideae, Neomangenotioideae. The Melioideae is richly represented by the Trichilieae and Turraeeae, but 5 tribes out of 7 are lacking. The Trichilieae is composed of 10 genera, 9 of which are palaeotropical (3 restricted to Asia, 4 to Africa sensu stricto); there are 4 genera in Madagascar: *Malleastrum* (12 spp.) endemic to Madagascar-Comores-Aldabra; *Astrotrichilia* (14 spp.) endemic to Madagascar; *Lepidotrichilia* (4 spp.) restricted to Madagascar and E. Africa; *Trichilia* (50 spp. in America, 14 spp. in Africa, some spp. in Madagascar and the Indo-Malayan region). The palaeotropical tribe Turraeeae is best represented in this part of the world: only 1 genus (*Munronia*) is endemic to Asia; *Naregamia* has 1 species in India, 1 in Angola; *Turraea* has 24 species in tropical Africa, 30–40 species in Madagascar, Mauritius and the

Comores, and about 6 species in tropical Asia and Australia. There are 2 genera endemic to Madagascar: *Humbertioturraea* (6–7 spp.) and *Calodecaryia* (1 sp.) and 1 genus is endemic to S. Africa: *Nymania* (1 sp.). The Swietenioideae-Swietenieae (9 gen.) is represented by genera in Africa and Madagascar, all of the endemic: *Khaya*, *Entandophragma*, *Pseudocedrela* and *Lovoa* in Africa sensu stricto, *Khaya* and *Neobeguea* in Madagascar; there are 2 genera in Asia-Malesia: *Soymida*, *Chukrasia*, and 2 genera in America: *Swietenia*, *Schmardea*. The Xylocarpeae is composed of 2 genera: *Xylocarpus* (2 spp.), a genus of mangroves and swamps confined to Indian Ocean coasts, included in the Madagascan region, and one African-American genus, *Carapa* (2–3 spp.) (Pennington & Styles, 1975; Leroy, 1977b).

To conclude about Meliaceae, strong endemism exists, at the subfaminial and generic levels in Madagascar and at the generic level in Africa. The Meliaceae is an ancient family represented in Africa sensu lato by 24 genera—that is nearly 50% of the whole family—18 of which are endemic. One genus (*Lepidotrichilia*) is common to Madagascar and E. Africa. The tribe Turraeeae seems centered on the Madagascan region; here *Turraea* has its highest number of species, and 3 genera are endemic to this region sensu lato: 2 to Madagascar, one to S. Africa. Furthermore, there is a link between *Capuronianthus* and Xylocarpeae.

Zygophyllaceae is a family of 25 genera and 200 species (Hutchinson, 1967), is mostly woody, and is distributed in dry regions of the two hemispheres, often in semideserts. It is represented by 2 genera in Madagascar: *Tribulus*, a widely spread genus, which there has 2 nonendemic species; *Zygophyllum*, a large genus confined in the Old World, especially in southern Africa, with 2 species endemic to Madagascar, one of them *Zygophyllum madagascariense* (Baill.) Stauffer, with a peculiar drupaceous fruit, can be considered as the type of a special subgenus. The two species occur sympatrically in the South Domain, generally on sands next to the sea.

Erythroxylaceae is a family of 3(–4) genera, the largest of which is *Erythroxylum* with about 200 species. This pantropical genus has about 30 species in the Madagascan region, all endemics. The other genera are: *Aneulophus* (1 sp.) and *Pinacopodium* (2 spp.) in tropical Africa and *Nectaropetalum* (perhaps a special family) with 9 species, 5 of which are endemic to Madagascar and still undescribed, the other 4 being endemic to Africa. *Nectaropetalum*, whose Madagascan presence is known thanks to Capuron's work (1963c), is a remarkable plant with imbricate and persistent sepals and dry and dehiscent fruits. It occurs in the dry regions in the north and northwest parts of the western Domain in Madagascar. *Aneulophus* is sometimes put in the Linaceae.

Lepidobotryaceae. Following Hutchinson (1967), this palaeotropical family is composed of 3 genera: *Sarcotheca* (10 spp.) in tropical Asia, *Dapania* (3 spp.) in Malaya and Madagascar (Veldkamp, 1967); *Lepidobotrys*, in Africa (Léonard, 1950). Thus, it presents an interesting distribution, but its naturalness is questioned (Airy Shaw, 1966; Veldkamp, 1967). Whatever it may be, the Madagascan plant, *Dapania pentandra*, is a very interesting species sharply

distinct, with flowers perfect, 5-staminate, and deprived of interstaminate scales (Huynh, 1971). According to Raven & Axelrod (1974), *Dapania* might have reached Madagascar by long-distance dispersal around the Indian Ocean. Let us note that this hypothesis, rather convincing as regards a genus whose fruits are readily dispersed, is consistent with a great antiquity for the Madagascan species.

Geraniaceae. Following Humbert (1959), this family is represented by 3 nonendemic genera: *Geranium* (2 spp. of the African section *Simensia*, 1 of which endemic); *Pelargonium* (1 endemic sp. of the S. African section *Ciconium*; 1 endemic species of the section *Peristera*, which extends from S. Africa to Australia, New Caledonia); *Monsonia* (an African genus with 1 species in secondary vegetation).

Oxalidaceae. This unrevised family comprises 2 nonendemic genera and 21 species (according to Baron, quoted by Humbert): *Biophytum* and *Oxalis.*

Linaceae is represented by 2 nonendemic genera: *Linum* (2 endemic spp.) and the palaeotropical genus *Hugonia* (5 endemic spp.).

Balsaminaceae is a family of 2 genera, 1 of which, *Impatiens*, occurs abundantly in Madagascar where 100 species or so have been recognized.

Ixonanthaceae, considered by many authors as a subfamily of Linaceae, is present in Madagascar with an endemic species of the genus *Allantospermum* (= *Cleistanthopsis*), which is bitypic, the other species occurring in Borneo. These species which were described independently in the same year 1965 by Forman for Borneo and Capuron for Madagascar, are both very similar to one another and well distinct: each of them must be considered as a subgenus of its own.

It is surprising enough that the palaeotropical family Irvingiaceae consisting of 3 genera, 1 of which, *Irvingia*, occurs in Africa and Southeast Asia, the other two being endemic to Africa, is absent from Madagascar. But the related genus *Allantospermum* has a distribution parallel to that of *Irvingia.* Plants of the group Irvingiaceae—Ixonanthaceae are a fundamental link between Africa-Madagascar on one hand an Southeast Asia on the other. Hence, I fully agree with Raven & Axelrod (1974) that it must proceed from "an west Gondwanaland plexus."

Malpighiaceae. This family of woody plants consists of 5 tribes, 65 genera, and 1,200 species (Hutchinson, 1967), mostly of South America. Some outliers, perhaps 15 genera or so, occur far from America. There are 10 genera in Madagascar: *Acridocarpus* (30–50 spp.) extends from tropical and S. Africa, Arabia, Madagascar to New Caledonia. *Caucanthus* is an African-Madagascan genus of 25 species. The endemic genera are: *Trichomariopsis* (1 sp.), *Philgamia* (3 spp.), *Calyptostylis* (1 sp.), *Microsteira* (28 spp.), *Rhynchophora* (1 sp.), *Digoniopterys* (1 sp.). *Sphedamnocarpus* is a Madagascan-African genus (8 sp. in S. and E. Africa, 12 sp. in the Madagascan region). *Tristellateia* is a palaeotropical genus (40 spp., 20 spp. in Madagascar, 1 in E. Africa, none in Australia). All these genera belong to two tribes: Hiraeeae, which contains 20 genera, 10 of which are endemic to S. America, and Banistereae (15 gen.). If we consider the

wholly family, 48 genera are endemic to America, 3 to Africa, 3 to Asia, and 6 to Madagascar. All Madagascan genera are either endemic or palaeotropical.

On the basis of the present evidence one can retain the idea that a post-Oligocene improverishment intervened in Africa and perhaps in Asia to eliminate part of Malphigiaceae, Madagascar playing its well-known role as a center of survival.

Vochysiaceae and Trigoniaceae. Plants of this group are chiefly represented in South America with 8 endemic genera and many species. But 1 genus, *Erismadelphus*, is present in tropical Africa (with 2 spp.), 1 in Madagascar *Humbertiodendron* (1 sp.), and 1 in S.E. Asia *Trigoniastrum* (1 sp.). Judging from this pattern of distributions with wide disjunctions and unbalanced proportions concerning the number of species, we may suggest that Vochysiaceae originated in Gondwana, the extant, extra-American genera clearly being relicts.

Polygalaceae. This family with a wide and mainly pantropical distribution is an ancient one consisting of 17 genera, 50% of which are endemic to America; it is poorly represented in Madagascar with only 2 genera: 20 endemic species of *Polygala* and 1 endemic species of *Carpolobia*, a Madagascan-African genus of 7 species (Breteler, 1969).

Araliaceae is a family (still unrevised for Madagascar) of 600 species distributed in 50 genera, chiefly tropical, with two principal centers in Southeast Asia and America. Its representation in Madagascar and the Mascarenes and the Seychelles is very important and of special interest, with 9 genera, including 4 endemic, and over 50 species. Hutchinson considers the family to be composed of 7 tribes, 4 of which are present in Madagascar: Cussonieae: *Cussonia* (25 spp. in tropical and S. Africa, Madagascar, Comores, Mascarenes), *Botryopanax* (endemic to the Mascarenes with 6 spp.), *Cuphocarpus* (a monotypic genus endemic to Madagascar). Panaceae: *Polyscias* (palaeotropical genus of 53 spp.; 8 spp. in Africa, 35 spp. in Madagascar-Comores, 8 spp. in the Mascarenes, 1 sp. in the Seychelles, 1 sp. in Ceylon); *Gastonia* (10 spp. in tropical and E. Africa, Madagascar, Mascarenes, Borneo, New Guinea . . .); *Schefflera* (a pantropical genus with 15 spp. in Madagascar-Comores, 13 spp. in Africa, 1 in the Seychelles, some spp. in Ceylon); *Sciadopanax* (a monotypic genus endemic to Madagascar); *Geopanax* (1 sp.) endemic to the Seychelles. Hedereae: *Neocussonia* (5 spp. in tropical and S. Africa, Madagascar). Plerandreae: *Indokingia* (a monotypic genus endemic to the Seychelles).

Several facts have to be emphasized: (1) the distribution of the genera into 4 tribes, of which 2 have a single representative. (2) The pattern of endemism with one monotypic genus special to the Seychelles, and one polytypic to the Mascarenes. (3) The very large number of *Polyscias* species in the Madagascan region. (4) The absence of *Schefflera* species in the Mascarenes, while numerous in Madagascar. (5) Two-thirds of the genera are African-Madagascan.

These facts, some of which remain rather enigmatic, support the hypothesis of the Madagascan region not only as a center of refuge but at the same time as an active center of speciation. Moreover, the family as a whole is well rooted in the African region.

Umbelliferae (275 gen., 2,800 spp.). This family is represented in Madagascar

by only 9 genera, 2 of which are endemic: *Anisopoda* (1 sp.) and *Phellolophium* (1 sp.); 1 is African-Madagascan, *Heteromorpha* (8 spp. endemic to Madagascar and a few in Africa); 5 are widespread: *Carum*, *Pimpinella*, *Caucalis*, *Sanicula*, and *Peucedanum*. There are 22 species of which 19 are endemic (Humbert, 1959). The interesting recent discovery of a *Lilaeopsis* species in Madagascar, Raynal, (1977) is surprising enough. This genus, which until now had 26 species with 16 American and the others from Australia and New Zealand, is a typically Gondwanian genus, which is absent from Africa. So a new problem is raised which is worth thinking about and analyzing.

VI

Loganiaceae. This family (as circumscribed by Leenhouts, [1962] of 26 [28] gen., 600 spp.) is represented in Africa and Madagascan by 11 genera, 5 of which are endemic. The Madagascan representation is important with 6 tribes (the family consisting of 7), 8 genera, and 70 species.

The genus *Anthocleista* (Potalieae) is restricted to tropical Africa and Madagascar with 14 species (4 in Madagascar), but its nearest ally is *Fagraea* from Asia and the Pacific. *Nuxia* (Buddlejeae) consists of 15 species in Africa (Leeuwenberg, 1975a), 11 species in the Madagascan region, of which 10 are endemic (including 1 in the Comores and 1 in the Mascarenes); its closest affinities are with the monotypic genus *Peltanthera* from Central and South America, and also with the monotypic genus *Androya*, endemic to Madagascar (Leenhouts). *Buddleja*, a large genus of more than 100 species (belonging to the same tribe), widespread in the tropics, except for Australia and the Pacific, is highly differentiated in Madagascar (8 spp., 1 of which is endemic to the Reunion) (Leeuwenberg, 1975b). The tribe Loganieae from Malaysia and the Pacific, reaches the Mascarenes with 2 endemic species of *Geniostoma*: *G. borbonicum* and *G. pedunculatum*. The small genus (6 spp.) *Mitreola* (= *Cynoctonum*) (American-Asian tribe, Spigelieae), which has a very extended and discontinuous area, is present in Madagascar with 1 endemic species, *M. turgida* Jovet. Three other species are confined to Asia, 2 of which are local endemics (Vietnam, Sabah); 1 species is endemic to the southern United States, and the sixth, *M. petiolata*, occurs in N. America, Brazil, Asia, Australia, and West Africa (Leeuwenberg, 1974). One African species of *Mostuea* (Gelsemieae), a genus of 8 species, 7 of which are in tropical Africa, occurs in Madagascar; the eighth species is known from Brazil. The eighth genus, *Strychnos*, is widely distributed in the tropics and subtropics with about 200 species, 15 of which are in Madagascar.

All these facts form a complicated whole from which several ideas can be drawn. First, Loganiaceae is an old family with a worldwide distribution in the tropics and subtropics of both hemispheres. Second, we have to take care not to explain every case in terms of the old and discontinuous distribution of the family. There is one endemic species of *Mostuea* in Brazil, two endemic species of *Geniostoma* in the Mascarenes, and some vast gaps in the area of *Mitreola* species, but we think no general and single explanation of this is to be sought. With respect to *Geniostoma* species from the Mascarenes, one must have in

mind that an extremely close ally, the genus *Labordia*, with as many as 20 species, is endemic to the relatively young island Hawaii.

Gentianaceae (80 gen., 900 spp.). This family is represented in Madagascar by 9 genera (50 spp., ¾ of which endemic), of which 2 are endemics: *Tachiadenus* (10 spp.) and *Gentianothamnus* (1 sp.). The genus *Chironia* is endemic to Africa-Madagascar. The other genera are palaeotropical (*Exacum*, 15 spp., *Sebaea*, *Canscora*) or widely spread (*Swertia*, *Eniscostemma*, *Neurotheca*). Let us note that the genus *Neurotheca* is present in the Madagascan swamps, with the widespread species, *N. loeselioides* (Guyana, Brazil, tropical and E. Africa) (Raynal, 1968).

Menyanthaceae (5 gen., 33 spp.). The only genus present in Madagascar is *Nymphoides* with 3 endemic species.

Lentibulariaceae (4 gen., 170 spp.) is a family of insectivorous water herbs widely distributed over the Globe. It has 2 genera in Madagascar: *Utricularia* (13 spp., 10 ? endemic) and *Genlisea* (an African-American genus with 4 spp. in Madagascar, 3 endemic). Because these plants are readily dispersed, they do not provide good material for biogeographical analysis.

Apocynaceae (250 gen., 2,000 spp., according to Markgraf, 1976). This is a family of wide distribution but chiefly pantropical, which is composed of 4 subfamilies, all of them represented in Madagascar. There are 23 genera in Madagascar (10 endemic) and 146 species (140 endemic). One genus, *Oistanthera* is endemic to the Mascarenes. The palaeotropical genus *Carissa* (Plumerioideae—Carissinae) has 9 species in Madagascar (7 endemic). In the same subfamily, the Carisseae—Landolphiinae is mainly represented by the pantropical genus *Landolphia*, which has a total of 60 species (13 endemic) in Madagascar and over 40 in Africa. There are 2 genera in the Rauwolfieae (a tribe of 12 genera, mostly in Asia)—Rauwolfiinae (a subtribe of 3 genera with a disjunct distribution): the pantropical genus *Rauwolfia* (5 endemic species) and the endemic genus *Cabucala* (18 spp.). The Plumerioideae—Alstonieae is interestingly represented by 4 subtribes: the endemic monotypic genus *Craspidospermum* is one of 2 genera constituting the subtribe Craspidosperminae, the other inhabiting Malesia. *Stenophagia* (Aspidospermatinae, a subtribe of 3 genera: 1 in America, 1 in Africa), with 5 species, is endemic. *Catharanthus* (Catharanthinae) is an isolated genus with 7 Madagascan species and 1 species in India. Two genera out of 4 in the Plectaneineae inhabit Madagascar: *Plectaneia* (12 spp.) endemic; *Gonioma* with 1 species in S.W. of Madagascar and 1 species in S. Africa.

The Apocynoideae has 4 genera in Madagascar, 1 of which, *Roupellina* (1 sp.), is endemic; *Mascarenhasia* is an isolated genus with 12 species, 1 of which reaches E. Africa; *Pachypodium* is an isolated, xerophilous genus with 17 species in Madagascar (12 endemic) and a few in E. and S. Africa.

Stronger endemism is offered by the Tabernaemontanoideae, which contains 4 endemic genera and another one almost endemic with 1 species also in E. Africa (*Hazunta coffeoides*).

A fact of special interest is that two monotypic subtribes of Apocynoideae

(Mascarenhasiinae, Pachypodiinae) are restricted to the Madagascan-E. African area.

Asclepiadaceae (one monotypic genus, *Trichosandra*, is endemic to Mauritius), *Solanaceae*, *Hydrophyllaceae* (cf. Humbert, 1959).

Convolvulaceae (*Humbertiaceae* included) (55 gen., 1,400 spp.). This is a family of wide distribution, but mainly of the tropics and subtropics, that is particularly abundant in America. There are 11 genera in Madagascar, of which 3 are endemic (cf. Humbert, 1959).

Boraginaceae (100 gen., 2,000 spp.) (cf. Humbert, 1959).

Callitrichaceae (1 gen., 30 spp.). The genus *Callitriche* is represented in Madagascar by at least 3 endemic species. None of the African or European species exists in Madagascar. Two species seem to have some morphological characters of S. America taxa (H. Schotsman, pers. comm.).

Verbenaceae (91 gen., 3,000 spp.). This family is well represented in Madagascar with 12 indigenous genera and 130 species (123 endemics). There are 2 endemic genera: *Adelosa* (1 sp.) and *Acharitea* (1 sp.), the latter being very close to *Nesogenes*, which also has 1 endemic species in the Madagascan region while the others occur in E. Africa and Polynesia. Another genus, *Coelocarpum*, has 5 Madagascan and 1 Socrotan species. If we add another genus common to Madagascar and Africa, *Chascanum* (30 spp. with 2 endemic in Madagascar and 28 in Africa) and 2 palaeotropical genera, *Holmskioldia* (10 spp. with 5 endemic in Madagascar) and *Premna* (200 spp., of which 13 occur in Madagascar, all but 2 endemic), we see that 7 out of 12 genera can be considered to be palaeotropical. The other 5 genera, 2 of which, *Vitex* and *Clerodendrum*, have respectively 39 species (38 endemic) and 62 species (endemic) in Madagascar, are pantropical.

In contrast with these large genera, the other 3 are also large genera but small in their Madagascan representation: *Phyla* (1 cosmopolitan sp.), *Priva* (1 endemic sp., 1 sp. common to Africa, 1 sp. common to Asia), and *Callicarpa* (1 endemic sp.).

Some very interesting facts have to be emphasized. First of all is the presence of 2 monotypic endemic genera, 1 of which, *Acharitea*, is akin to *Nesogenes* (6 spp.), a genus with an extraordinary distribution in E. Africa-Comores-Seychelles-Mascarenes-Madagascar and Polynesia. The two genera belong to a group, a family of its own according to some authors (Dicrastylidaceae), which is essentially Australian (*Physopsis*, *Lachnostachys*, *Dicrastylis*, *Mallophora*, . . .). All of these genera are closely related to Verbenaceae—Stilboideae, a small subfamily of 5 monotypic genera, endemic to S. Africa. Therefore, there is a link, which seems ancient, between Madagascan and Australian Verbenaceae.

Another fact is that there is a littoral species of *Vitex*, *V. trifolia*, which covers a large area around the Indian Ocean from E. Africa to Japan and Australia. It represents, of course, a category different from that of *Calophyllum inophyllum*. The former has surely nothing to do with other species such as this one, which should be considered as a possible pioneer species. Another species, *Phyla nodiflora*, belonging to an American genus, occurs here and there, on sandy beaches and also at higher elevations, preferentially on calcareous soils.

Labiatae (in particular, one monotypic genus, *Mahya*, is endemic to Réunion), *Avicenniaceae*, *Plantaginaceae* (cf. Humbert, 1959).

Oleaceae. This family of 29 genera and 600 species is widespread over the World, especially in temperate and tropical Asia. There are 62 Madagascan species (60 endemic) and 5 genera, of which 2 are endemic to the Madagascan region: *Noronhia* (40 spp.) and *Comoranthus* (2 spp. in Madagascar and one in the Comores). The other genera are: *Olea*, an Old World genus with 20 species, of which 4 (3 endemic) occur in the Madagascan region. Two large tropical and subtropical genera: *Linociera* (1 sp. endemic to Madagascar and 1 endemic to the Comores), and *Jasminum* (9 spp., 8 endemic).

Scrophulariaceae (unrevised family; cf. Humbert, 1959; 2 genera, *Allocalyx*, 1 sp., *Bryodes*, 3 spp., are endemic to the Mascarenes).

Myoporaceae. This small family of Bignoniales deserves special attention. It is composed of 4–5 genera, 2–3 of which occur in S. Africa-Madagascar. Only one genus, *Myoporum* (30 spp.) has a wide distribution from Australia and the Pacific Islands to Japan and E. China and even the Mascarenes (1 sp., endemic). The other genera are: *Pholidia* (40 spp.), endemic to Australia; *Bontia* (1 sp.), endemic to the West Indies; *Ranopisoa* (1 sp.), endemic to Madagascar (Leroy, 1977d) and, when admitted in Myoporaceae, *Oftia*, 3 species endemic to S. Africa. *Ranopisoa* was described as *Oftia* by Capuron (1972a), but I have shown that it is distinguished from the latter by some characters. Whether or not *Oftia* belongs in this family or in Scrophulariaceae is not yet established, but in any case, it is at least an ally.

Thus, there is evidence from the pattern of distribution of the Myoporaceae, along with those from Cunoniaceae and other austral families, that their geographical origin might have been in any part of Gondwanaland. Moreover, the Myoporaceae, although having reached a high taxonomic level, might have originated before the breakup of Gondwanaland. However, the wide distribution of the genus *Myoporum*, obviously post-Gondwanian, might result from long-distance dispersal during Tertiary times.

Gesneriaceae (120 gen., 2,000 spp.). This is a family divided into 2 subfamilies, Gesneroideae and Cyrtandroideae, the former principally American (with some Australasian genera), and the latter principally tropical Asian and African and also European and even Australasian (*Cyrtandra*, . . .); it is represented in Madagascar by 3 genera: *Streptocarpus*, a genus endemic to Africa-Madagascar, with 41 species in Madagascar, all of them endemic and 90 species in Africa, almost all in S. and E. Africa; *Didymocarpus*, a genus widely distributed in warm regions (150 spp.) having 1–3 species in Africa and 3 endemic species in Madagascar; *Colpogyne*, an endemic monotypic genus (Burtt, 1971).

Bignoniaceae (120 gen., 650 spp.). In Madagascar this family, is represented by 2 tribes, out of 4 constituting the family (Schuman, 1895), and 10 genera. It displays an old distributional pattern of great interest with respect to the tribe Crescentieae, which is composed of 11–12 genera: 5–6 in Madagascar, all of them endemic, 5 in America, and 1 in Africa. This distribution is especially noteworthy as the 5–6 Madagascan genera form a homogenous group, with, it

seems, some distinctive evolutionary trends. If we put the genera with unilocular stamens aside (*Ophiocolea*, 5 spp. and *Colea*, 20 spp.), the other 3–4 genera, although well defined, are very close to one another. In my opinion, *Rhodocolea* might be the most primitive, particularly *R. perrieri* Capuron with its perfect actinomorph flowers and pentastaminate androecium (it even might be raised to the generic level). Next to *Rhodocolea* is *Phylloctenium*, then *Phyllarthron*, a plant whose leaves are reduced to an articulated rachis. Two species of the latter (discovered and described by Capuron, 1960, 1970a) offer such an extraordinary floral zygomorphism that I (Leroy, 1972) proposed to base a new genus *Paraphyllarthron*, upon them. Whether accepted or not as taxon by subsequent authors does not matter, what is important is that it descended from *Phyllarthron*, a taxon still in existence today in the same country. The genus *Phyllarthron* itself was possibly derived from a *Rhodocolea*-like taxon, now extinct. The Madagascan Crescentieae are possibly a group of closely related genera that have originated in Madagascar during post-Gondwanian time.

The tribe Tecomeae has 4 genera in Madagascar: *Perichlaena*, a monotypic and endemic genus very close to *Fernandoa*. *Fernandoa*, a genus of 6 species of which 3 are endemic to Madagascar and 3 endemic to tropical Africa (Gentry, 1975). *Rhigozum* (1 sp. in Madagascar, 3 spp. in South Africa). *Stereospermum*, a palaeotropical genus with 9 species in Madagascar (constituting a distinct section, confined to the western Domain).

The family Bignoniaceae in Madagascar seems to offer a typical case of post-Gondwanian evolution or taxogenesis from some ancestors, now extinct, common to Africa and South America.

Acanthaceae (250 gen., 2,500 spp.). In Madagascar there are 57 genera, of which 22 are endemic, and more than 400 species, 375 of which are endemic. Eleven genera are African-Madagascan with 47 species in Madagascar, 42 of which are endemics. Five genera are related to African genera. The other genera are palaeotropical or pantropical: *Justicia*, 95 species in Madagascar, 90 of which are endemic with African affinities; *Hypoestes* 80 species, 78 of which are endemics. On the whole, affinities with the African flora are obvious; those with the Asian and Malaysian floras are rather modest (Benoist, quoted by Humbert, 1959).

Several remarks deserve attention: The very high degree of generic endemism is noteworthy in Madagascar. Moreover, the distributional pattern of several genera is of a particular interest. The genus *Stenandriopsis* (5 spp. in tropical west Africa, 1 in E. Africa, 8 in Madagascar) is closely allied to *Aphelandra* (200 spp. in tropical America; Heine, 1963; Stearn, 1971). The genus *Mendoncia*, which is mostly S. American (90 spp.), has 4 species in Africa (Gabon & Ivory Coast) and 3 in Madagascar. It is closely related to the monotypic genus *Gilletiella*, endemic to Congo-Angola, so much so that Bremekamp proposed to link the two genera in the new family Mendonciaceae. The genus *Justicia* occurs likewise in S. America and Africa-Madagascar. *Oplonia* is Madgascan-American (9 spp. in the West Indies, 5 spp. in Madagascar), but absent from Africa (Stearn, 1971). All these factors indicate that the family, evolu-

tionarily advanced as it is, might have had a Gondwanian origin (perhaps by the close of the Cretaceous).

Pedaliaceae. This small family (12 gen.) is almost completely confined to warm regions of the Old World, especially Africa where 9 genera are endemic. *Uncarina*, endemic to Madagascar, is a genus of shrubs with thick branches and contains 9 species, all of them more or less xerophilous and occuring in the Occidental Domain (Humbert, 1962). Several species belonging to other genera have been introduced: *Dicerocaryum zanguebarium*, a monotypic genus of E. and S. Africa and Rhodesia, Angola; *Sesamum* sp.; *Martynia* (= Martiniaceae Stapf., an American family of 3 genera) *annua*, introduced from Mexico into Africa and Madagascar. An annual herb of African sandy beaches, *Pedalium murex*, is also in Madagascar and reaches Ceylon and India.

Campanulaceae (*Lobeliaceae* included) is a family (60 gen., 1,500 spp.) with worldwide distribution, but particularly in the Mediterranean region and S. Africa, and also in the Tropics. There are 30 species (26 endemic) and 7 genera (3 endemic) in the Madagascan region. Four genera belong to Lobelioideae: *Heterochaenia* (a genus consisting of 3 spp. endemic to Réunion), *Dialypetalum* (endemic to Madagascar, 5 spp.), *Monopsis* (a genus of tropical and S. Africa with 1 sp. on the Comores), *Lobelia* (a widespread genus [300 spp.], mostly tropical and subtropical, richly represented in Africa and America with 12 species in Madagascar [9 endemic] and 7 species in the Mascarenes [2 endemic]). There are 3 genera of Campanulaceae sensu stricto: *Berenice* (a monotypic genus endemic to the Reunion—Badré et al., 1975), *Gunillaea* (an African-Madagascar genus with 1 species endemic to Africa, 1 common to E. Africa and Madagascar), *Wahlenbergia* (a widespread genus but mainly of the S. hemisphere with 200 species 11 of which in Madagascar (4 endemic) (M. Thulin, unpublished paper, 1977).

It is of special interest that 2 genera are endemic to the Mascarenes, and monotypic: they seem, therefore, to be vestigial.

Goodeniaceae. This family of 14 genera and 300 species is almost exclusively austral but its Madagascan representation, 1 genus, *Scaevola*, with 2 species widespread along sea coasts all over the Globe, has no special significance.

Rubiaceae (500 gen., 5,000 spp.). This is a pantropical and subtropical family represented in Madagascar by its 3 subfamilies and about 21 tribes (Psychotrieae, Morindeae, Triainolepideae, Pauridiantheae, Craterispermeae, Knoxieae, Paederieae, Hedyotideae, Cruckshanksieae, Lathraeocarpeae, Anthospermeae, Spermacoceae, Rubieae, Naucleeae, Cinchoneae, Mussaendeae, Gardenieae, Ixoreae, Alberteae, Vanguerieae, Guettardeae). There are about 70–80 genera, 25–30 of which are endemic (2 new genera recognized by Capuron await description), and more than 600 species, nearly all of them endemic. As was emphasized by Bremekamp (Humbert, 1959), the Madagascan Rubiaceae have much stronger affinities with the African flora than with the Asian one. Some genera (*Triainolepis*, *Alberta*, . . .) are restricted to Madagascar and E. and S. Africa. Some tribes are particularly well represented in Madagascar: Psychotrieae (ca. 11 gen., 5 endemic), Hedyotideae (5 gen., 2–3 endemic), Spermacoceae,

Naucleeae (a tribe of 8 genera, 5 endemic in Madagascar), Ixoreae (8–12 genera, several of which endemic), Gardenieae (4 gen., 2 endemic—Leroy, 1974). There is one endemic genus in the Madagascan Cinchoneae, and another one in the Mussaendeae. Three genera are endemic to the Mascarenes: *Scyphochlamys* (1 sp.), *Neoschimpera* (1 sp., Seychelles), *Fernelia* (2 spp.).

Many data concerning the Madagascan Rubiaceae are contained in an important unpublished paper by Capuron, but it is, however, impossible to draw any serious conclusion before the revision of the family is completed.

Compositae (900 gen., 15,000 spp.). This is a very large family of cosmopolitan distribution. It ranks first in the S. African flora with 174 genera and 2,072 species (Goldblatt, this symposium). It is also first in Madagascar with 87 genera (13 endemic) and 550 species (500 endemic) distributed in 9 tribes (none of which endemic). Two monotypic genera are endemic to the Mascarenes (*Eriothrix*, *Cylindrocline*). The Madagascan Compositae are strongly linked with the E. and S. African ones (cf. Humbert, 1959).

VII

Concerning the Madagascan Monocots I shall be content with recalling some of the outstanding classical facts, supplemented with some recent results. It is well known, for example, that the Bambuseae, Palmae, Pandanaceae, and Orchidaceae have a particularly important Madagascan representation.

A. *Alismatidae*.—Among the represented families: Alismataceae, Aponogetonaceae, Scheuchzeriaceae, Najadaceae, Potamogetonaceae, Hydrocharitaceae, Triuridaceae, only the latter has an endemic Madagascan genus, *Seychellaria* (1 sp. in Madagascar, 1 sp. in the Seychelles). The Triuridaceae (7 gen., 80 spp.) are herbaceous terrestrial mycotrophic plants with apocarpous flowers and albuminous seeds.

B. *Commelinidae*.—The Bamboos are impressively represented in Madagascar with 10 genera, 6 of which endemic. One of the latter, *Nastus*, has 12 species in Madagascar, 1 in the Réunion. Three are monotypic: *Hitchcockella* (which is related to both *Nastus* and the American genus *Chusquea*), *Decaryochloa* and *Pseudocoix*. The other 2 genera are *Hickelia* (2 spp.) and *Perrierbambus* (2 spp.) (which would be related to an American genus [Humbert, 1959]).

The nonbambusoid tribes of grasses taken as a whole are represented in Madagascar by 132 genera, 15 of which are endemic, and 500 species. Two genera constitute by themselves two tribes apart: *Cyphochlaena* (Boivinelleae) and *Lecomtella* (Lecomtelleae) (J. Bosser, pers. comm.). Thus there is some indication of an active and ancient differentiation of grasses, perhaps since the Eocene. A study restricted to the Malagasy fodder grasses was published by Bosser (1969).

Cyperaceae (90 gen., 400 sp.). There are 29 genera and 350 species (60 endemic) in Madagascar (cf. Humbert, 1959). In particular, the genus *Costularia* is to be cited: it is composed of 14 species, 11 of which occur in Australia, and 3 in S. Africa and Madagascar.

Strelitziaceae (3 gen., 7 spp.). This is a family, formerly merged into

Musaceae, whose distribution is strictly austral and strongly discontinuous, with *Ravenala*, a monotypic genus, in Madagascar, *Strelitzia* (5 spp.) in S. Africa, and *Phenakospermum* (2 spp.) in S. America. One genuine species of the palaeotropical family Musaceae (*Ensete* sp.) inhabits Madagascar.

Commelinaceae (38 gen., 500 spp.). Two genera are of special interest: *Coleotrype* with 5 endemic species in Madagascar, 1 species in S. Africa, and 1 in W. tropical Africa; *Pseudoparis* (2 spp.), a very isolated endemic genus.

Eriocaulaceae (13 gen., 1,200 spp.) is a family of extreme biogeographical interest whose area is almost entirely confined to tropical and subtropical America. There are only 2 genera endemic to Africa-Madagascar: *Mesanthemum* with 2 species in Madagascar and 6 in Africa; *Moldenkeanthus*, a monotypic genus endemic to Madagascar. Aside from *Eriocaulon*, a large genus which has 19 species in Madagascar (10 endemic), the other 2 genera are American with only 1 or 2 species in Africa and Madagascar (*Paepalanthus*, *Syngonanthus*). The endemic genus *Moldenkeanthus* is very close to *Paepalanthus* and the strictly American genus *Leiothrix* (Morat, 1976).

Zingiberaceae (45 gen., 700 sp.). This family, especially well developed in Indo-Malesia, is represented by 6 nonendemic genera in Madagascar, 1 of which, *Aulotandra*, has 5 species (4 Madagascan and 1 in W. tropical Africa).

Typhaceae, Juncaceae (cf. Humbert, 1959).

C. Arecidae.—Palmae (220 gen., 2,500 spp.). The Palmae (Arecales), whose fossil material is known from the Upper Cretaceous, are one of most noteworthy features of the Madagascan flora. There are 18 indigenous genera, 15 of which are endemic, and 120 species, all but 2 endemic (Humbert, 1959).

The palms occur also in the Seychelles (6 endemic gen.: the famous Borassoid *Lodoicea* possibly related to the Malayan *Borassodendron*, and 5 spiny Arecoid gen.) and Mascarenes (6 endemic monotypic gen.) (Corner, 1966). According to Corner, Madagascar "acting as a small continent of long isolation has evolved new species of undergrowth palms from its Arecoid heritage, but it has not produced a subfamily or a new manner of palm life." However, such Borassoid genera as *Medemia*, *Latania*, and *Lodoicea* are Gondwanian relicts (Corner).

Pandanaceae (3 gen., 700 spp.). The abundance of *Pandanus* species is also a striking feature of the Madagascan flora which counts 30 species, nearly all of them endemic (Mascarene included).

Araceae (100 gen., 2,000 spp.) are of a particular interest with respect to taxogenesis for, aside from the pantropical genus *Pistia* and some introduced species (*Alocasia* sp., *Caladium* sp., *Zantedeschia* sp.), they are represented in Madagascar by two elements:

1. An autochthonous highly differentiated element composed of 2 endemic tribes and 4 genera: (a) Typhonodoreae (Philodendroideae): 1 genus, *Typhonodorum*, which reaches Pemba and Zanzibar. (b) Arophyteae (Aroideae), including *Carlephyton* (3 spp.), *Colletogyne* (1 sp.), and *Arophyton* (7 spp.).

2. An oriental element marked by the presence of an endemic species of

Amorphophallus (*A. hildebrandtii*), and secondarily by some natural, naturalized, and/or cultivated species (*Remusatia vivipara*—which reaches Africa, *Typhonium divaricatum*, *Pothos scandens*, *Amorphophallus campanulatus*, and *Colocasia esculenta*).

All in all, there are 13 endemic species.

Lemnaceae (cf. Humbert, 1959).

D. Liliidae.—Pontederiaceae (6 gen., 30 spp.) is represented in Madagascar by one monotypic genus, *Schlleropsis*. This genus had been considered to be a Madagascan endemic until 1967, when Letouzey and Bosser (Letouzey, 1967) reported its presence in Cameroon. The Pontederiaceae are easily dispersed water plants, however, *Schlleropsis* might be an ancient genus in its African-Madagascan area.

Liliales. Any serious biogeographical judgement on the Liliaceae, together with many other closely allied families, would need a careful review of a great many publications, among them that by Huber (1969). I only intend to give indications on some selected families.

The Herreriaceae (which is a subfamily of Liliaceae for many authors), close to Asparagaceae, is composed of 3 genera: 1 in Madagascar (*Herreriopsis*, 1 sp.), 1–2 in S. America (*Herreria*).

Asteliaceae is a family of some genera (*Yucca*, *Dracaena*. . .), 1 of which, *Cohnia*, with fleshy fruits, has 3 species ranging from the Mascarene Islands to New Caledonia.

Dianellaceae is an Australasian family with 2 genera: *Dianella* in Asia, Hawaii, and Madagascar (Raven & Axelrod, 1974) and *Excremis* in S. America.

Asphodelaceae. The genus *Arthropodium* has 1 species in Madagascar, the others in Australia and Pacific Islands. *Lomatophyllum*, an endemic genus with fleshy fruits, has 10 species in Madagascar, 3 species in the Mascarenes. *Aloe*, an African-Madagascan genus, chiefly developed in Madagascar, where it has 30 endemic species, and oriental and austral Africa.

Liliaceae-Scilloideae has 1 endemic genus: *Rhodocodon* (8 spp.).

Iridaceae. The endemic monotypic genus, *Geosiris*, is obviously a relict.

Velloziaceae (5–6 gen., 200 spp.) is a small, typically occidental-austral family composed of 2 genera: *Xerophyta* in Madagascar and Africa and *Talbotia* S. Africa and 4 in South and Central America (Smith & Ayensu, 1974). *Talbotia* is a monotypic genus. The genus *Xerophyta* is divided into 3 sections. One of these, section *Xerophyta*, is endemic to Madagascar with 2 species. The second section is common to Africa (1 sp. endemic to Madagascar, 10 endemic spp. in Africa, some of them reaching Zaïre and Ethiopia). The third section is endemic to Africa (14 spp.).

Dioscoreaceae (4 gen., 650 spp.) is represented in Madagascar by 2 genera: *Dioscorea* (over 30 spp., 27 endemic) and 1 monotypic endemic genus, *Avetra*, certainly primitive with a vestigial rhizome, which has completely disappeared in *Dioscorea*. Another genus, likewise monotypic but Indonesian, *Trichopus* (Trichopodaceae) is generally considered as related.

Taccaceae (cf. Humbert, 1959).

Orchidaceae (740 gen., 20,000 spp.). This is one of most important families

in the Madagascan flora with about 1,000 species and 56 genera, about 10 of which endemic. Some genera are widely distributed: *Bulbophyllum*, *Eulophia*, *Oecoeclades*, ... Certain others have a much higher number of species in Madagascar than in Africa: *Angraecum*, *Jumellea*, *Aeranthes*, *Cynorkis*, *Benthamia*. The Asian affinities are weaker than the African ones (J. Bosser, pers. comm.).

In conclusion, many data can be drawn from the analysis of the Madagascan Monocots to form the basis for certain useful conclusions. The occurrence of isolated and highly differentiated genera such as *Medemia*, *Latania*, *Lodoicea*, *Seychellaria*, *Geosiris* (a family of its own for some authors), *Avetra*, as well as that of endemic tribes, namely Boivinelleae and Lecomtelleae in nonbambusoid grasses, and Typhonodoreae and Arophyteae in Arales, appears to support the hypothesis of a Madagascan-African origin for many Monocots by, most likely, the close of the Godwanian epoch or early in the Tertiary. Further, the fact that such high level taxa as Bambuseae, Palmae, Pandanaceae, Orchidaceae, are particularly well represented in Madagascar might, in part, be explained by referring to a serious impoverishment of the African flora from Miocene times onwards. In many cases, of course, e.g., those of Orchidaceae (*Angraecum*, *Jumellea*, *Aeranthes*, *Cynorkis*, *Benthamia*), Palmae (the group including *Dypsis* with 21 spp., *Neophloga* with 30 spp., *Chrysalidocarpus* with 20 spp. . . .), and Poaceae, we do not deal with an ancient differentiation but with a secondary one: it is the young part of the Madagascan element. The genera *Dypsis*, *Neophloga*, and *Chrysalidocarpus* are closely allied and have certainly had a common ancestor in Madagascar. Others, such as those of the fan-leaved subfamily Borassoideae seem being genuinely Late Gondwanian elements: *Medemia* (1 sp. in Madagascar, 1 sp. in E. Africa); *Latania* (3 spp.); *Lodoicea* (1 sp.) related to *Borassodendron* of S.E. Asia (Corner, 1966); *Borassus* (5 spp. ? of which 2 in Madagascar, 1 in Africa, 1 in Asia, 1 in New Guinea); *Hyphaene* (more than 10 spp. in Africa and Madagascar). The ancestors of these Borassoid genera must have been dwellers of the Gondwanian Africa.

VIII

Pteridophytes (F. Badré, pers. comm.; Christensen, 1932).—Most of the genera are represented in the Mascarene region, except for the primitive ones such as *Matonia* (Malaysia, Borneo, Sumatra), *Dipteris* (Asia), and *Loxsoma* (New Zealand). The Mascarene region is known for its high number of endemic species: 200 out of a total of 550. The greater part of the Pteridophytes from the Mascarene region is related to representatives from Asia (and particularly from Indomalaysia). According to their affinities, Christensen (1932) recognized 7 groups of species:

(1) The Mascarene element: about 70 species, mostly belonging to groups of species within large genera such as *Cyathea*, which contains 37 species, almost all of them endemic. Several large genera have only 1 or a few endemic species. There are 2 endemic and monotypic genera: *Psammiosorus* (confined to Madagascar) and *Ochropteris*.

(2) The African element: about 92 species (Christensen). Here belongs also the genus *Mohria* (2 spp. in Africa, Madagascar, and Réunion). Let us cite also the genera *Blotiella* with 1 species in America and 16 in Africa, Madagascar and the Mascarenes, and *Actiniopteris*, which is however also present in India (2 spp. out of 5).

A markedly disjunct area is shown by *Elaphoglossum hirtum* (tropical America, Réunion, Madeira, Azores) and *Pellea calomelanos* (Spain, E. and S. Africa, N. India, Madagascar, Réunion).

(3) The Eastern (African-Malesian) element: represented by more than 150 species, that is, nearly ¼ of the total number. Examples include *Angiopteris* (from Madagascar and Réunion, with 1 species in Japan and Polynesia), *Drynaria* (about 20 spp. in Asia and Australia, 1 sp. in Madagascar and Mauritius), *Loxogramme* (35 spp. in Asia with 2 spp. in the Mascarene region, 1 of which also in Africa), *Microsorium*, particularly well represented in tropical Asia (4 spp. in the Mascarene region, 2 of which are endemic), *Davallia* (40 spp. mainly Asian and Polynesian, 1 in Africa, Seychelles, Rodrigues, Mauritius, and Madagascar). Several species are widely distributed, occuring also in Central and Eastern Asia. Examples include *Dryoathyrium boryanum* (Africa, Madagascar, Mascarenes, Asia, Polynesia), *Diplazium sylvaticum* (Mauritius, Asia, Philippines).

(4) The Western (American-African) element: about 85 species (18% of the total number of Pteridophytes). Here belong such genera as *Elaphoglossum* (400 spp., most of which occur in America, 40 spp. in the Mascarene region), *Doryopteris* (35 spp., mainly in S. America, 2 of which are endemic), *Pellea* (75 spp., most of which occur in S. America, 30 spp. in Africa and the Mascarene region), *Trachypteris* (2 spp., 1 of which occurs in S. America and the Galapagos Islands, the other in Madagascar).

(5) The Southern element: represented by 15 species belonging to such genera as *Blechnum*, *Schizaea*, *Gleichenia*, ...

(6) The pantropical element with about 20 species.

(7) The cosmopolitan element: about 15 species, including *Osmunda regalis*, *Lycopodium clavatum*, *Pteridium aquilinum*, *Pteris cretica*, *Pteris vittata*, *Equisetum ramosissimum*, *Cystopteris fragilis*, *Adiantum capillu-veneris*, *Hymenophyllum tunbrigense*. . . .

From that rather artificial classification it becomes clear that the palaeotropical element is best developed in the Mascarene flora. Also that the number of endemic species in the Mascarene region is proportionally high, whereas only a few of the genera are endemic. This is a general feature of the Mascarene flora which is characterized by a very strong specific endemism.

Gymnosperms.—Podocarpaceae (8 gen., 150 spp.). This family of Coniferales, almost confined to the tropical southern hemisphere, is represented in Madagascar by the only genus *Podocarpus* (100 spp.) with 6 endemic species. This genus was divided into 8 sections (Buchholtz & Gray, 1948), 1 of which is endemic to S. Africa. The Madagascan species belong to section *Eupodocarpus* (with transfusion tissue) which is present also in Africa, but also in S. America, Australia, South Pacific Islands and Asia.

Cycadaceae (1 gen., 10 spp.). The genus *Cycas*, confined to the Indian Ocean and western Pacific, is represented in Madagascar, the Comores, and E. Africa (Tanzania, Mozambic) by 1 special species (*C. thouarsii*) which grows along sea coasts, often in the *Barringtonia* formations.

General Conclusions

In every stage of its evolution, whether it be primitive, advanced, or intermediate, the Madagascan vascular flora is of outstanding originality. No doubt, this is due in part to extremely diversified ecological conditions, but also, and above all, to the fact that the island which was part of the Gondwanaland continent, was hardly modified in the course of time, at least since the early Cretaceous. In contrast, most of the same flora that occupied continental Africa became greatly impoverished, particularly from the Miocene on, due to climatic changes.

Therefore, Madagascar now appears to be an African fragment that has not only been an extraordinary area for the differentiation of taxa but above all both a refuge for every kind of immigrant and a center of survival for archaic autochthonous plants. Its relationship with East and South Africa is obvious and represents an especially interesting kind of affinity because it testifies to the peripheral character of this region compared to the African landmass; it also testifies to the antiquity of the Madagascan flora. That this relationship really exists is supported by many facts, by far the most convincing of which is the occurrence in the Madagascan region sensu lato of a close-knit group of two austral families with monosulcate or monosulcate-derived pollen, belonging to Magnoliales: the Winteraceae and Canellaceae. The former is divided into two subfamilies, one with 7 genera in the Pacific area and 1 in tropical America; the other subfamily is unispecific and endemic to Madagascar. The Canellaceae comprises 5 genera, 1 endemic to Madagascar, 1 to South Africa, and 3 to tropical America. Linked to these two families of Magnoliales, absent from the interior of Africa is the Monimiaceae which is likewise austral, and especially richly represented in Madagascar. Equally significant in the austral Magnoliales is the Hernandiaceae (4 gen.); *Hernandia* consists of several subgenera, 2 of which are most primitive, 1 of them is endemic to Australia, the other to Madagascar.

It is also noteworthy that the primitive Hamamelididae is represented in the same area by 2 endemic genera of Hamamelidaceae (none in the interior of Africa) and, if admitted in this subclass, by several special families such as the Myrothamnaceae and Didymelaceae.

Another striking fact is the very strong endemism of the Dilleniidae, not only at the generic level, but also at the familial one: 5 endemic families (Diegodendraceae, Sphaerosepalaceae, Sarcolaenaceae, Asteropeiaceae, Medusagynaceae); several families with an exceptional development (Malvales, Flacourtiaceae, Sapotaceae, Ebenaceae, . . .). The taxonomic level is roughly rather higher than that of Megnoliidae and in many cases speciation is active.

The Rosidae are also to be noted. Such families as Brexiaceae, Montiniaceae,

and Escalloniaceae are austral families and not or hardly represented in continental Africa sensu stricto. The Proteaceae, an austral family of 75 genera, is concentrated in Australia (45 gen.) and South Africa (14 gen.), but it has 3 genera in Madagascar, 2 of which are endemic. The Balanophoraceae, again an austral family, has been divided into 6 subfamilies, 2 of which are endemic to Africa, principally South Africa; the subfamily Helosioideae to which belongs the Madagascan genus *Ditepalanthus*, is absent from Africa and present in Asia (3 gen.) and America (3 gen.).

The Asteridae which is evolutionarily more advanced is also richly represented in Madagascar, but contrary to the facts mentioned above, its endemism is in general rather at a lower level. There is almost a rule: as one goes down taxonomic levels, speciation becomes more active. Perhaps not a single endemic family of Asteridae is present in Madagascar whereas such genera as *Clerodendron*, *Justicia*, *Coffea*, *Helichrysum*, *Vernonia*, *Senecio*, etc. have many endemic species.

With respect to Monocotyledons, it is difficult to draw any homogenous conclusion because the taxogenetic knowledge of this group is rather poor. Roughly, however, the facts are comparable. There is on the one hand, a very important archaic element including relictual endemic subfamilies, tribes, and genera and, on the other hand, a younger element with neo-endemic genera and a huge number of endemic species that result from an expectionally active speciation (Orchidaceae, Gramineae, . . .).

As a whole, the Madagascan vascular flora is considered here as an autochthonous flora that has differentiated principally from the original Gondwanian stock and has, in course of time, grown rich through evolution of its members and immigration of newcomers through long-distance dispersal.

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SYSTEMATICS OF *FLAVERIA* (FLAVERIINAE—ASTERACEAE)[1]

A. Michael Powell[2]

Abstract

Twenty-one species are recognized for *Flaveria* in this first revision of the genus since 1915. Three new species are described. Morphological, cytological, chemical, and artificial hybridization approaches were used in the study. Interspecific crosses revealed both weak and strong reproductive barriers among various species of *Flaveria*, *Sartwellia*, and *Haploësthes*. *Flaveria* includes both self-compatible and self-incompatible species, some of which exhibit C_4 photosynthetic metabolism, and all of which produce sulfated flavonoids.

Most of the 21 species of *Flaveria* are native to North America where the taxa occur in Florida and adjacent states, in Kansas-Colorado, south through Texas, New Mexico, and Arizona in the United States, and throughout most of Mexico to Yucatán. Three species also occur in the West Indies, Greater Antilles, and South America, with two weedy taxa extending to Africa and India. One species is restricted to Australia.

The Flaverias have a strong preference for alkaline or gypseous soils, and frequently exist under disturbed conditions. The species in Florida occur only in alkaline soils at pH 7.2–8.2 (Long & Rhamstine, 1968). A few species, particularly the weedy *F. trinervia* and *F. bidentis*, may occur in various soil types. In the arid southwestern United States and northern Mexico the species are commonly found in moderate to strong saline or gypseous soils close to permanent or ephemeral water sources such as rivers, creeks, irrigation canals, fields, roadsides, ponds, and bolsons. The distribution of most species consists of colonies that are somewhat localized and spotty throughout the range. Seldom do Flaverias exist in continuous populations, except with coastal taxa where the habitats are continuous. Accordingly, most species are endemic, as though restricted by localized or regional edaphic and climatological features.

This is the first comprehensive study of *Flaveria* since Rydberg (1915) recognized 16 species of the genus in his treatment of Helenieae for the *North American Flora*. The account by Rydberg is strikingly different from the original mono-

[1] I have deep appreciation for the curators of herbaria from which specimens were borrowed. The National Science Foundation kindly supported this work through grants GB-37674 and BMS 73-06851 A01. I thank B. L. Turner for having an interest in *Flaveria*, for his informative discussions regarding relationships of the genus, and for providing seeds and buds of several species. I thank Walter V. Brown for collecting and bringing to me living plants of *F. floridana*, and for sharing provocative phylogenetic ideas based upon his investigations of C_4 photosynthesis and Kranz anatomy in *Flaveria*. I am grateful to R. M. King for assistance in gathering literature, and for helping to provide mounted specimens of my own collections for study; to R. H. Hartman for providing material of *F. pubescens* and *F. pringlei*; to Tom Mabry and Munira Al-Khubaizi for organizing and carrying out preliminary chemical studies of Flaveriinae; to James F. Weedin for providing excellent and conscientious technical assistance; to Marshall C. Johnston for the Latin translations; to Michael Theroux, Don Pinkava, and David Keil for providing material for the propagation of *F. mcdougallii*; and to Emily Lott for reviewing the manuscript.

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Ann. Missouri Bot. Gard. 65: 590–636. 1978.

0026-6493/78/0590–0635/$04.75/0

graphic account of *Flaveria* in which Johnston (1903) recognized 15 species. Three species, one each from Mexico, Florida, and Arizona have been described since 1915, and three additional species, two from Mexico and one from Texas, are described in the present treatment.

Flaveria is related to *Sartwellia* (Turner, 1971) and *Haploësthes* (Turner, 1975). These three genera constitute the subtribe Flaveriinae which belongs in or near Senecioneae in the opinion of Powell & Turner (1974). Rydberg (1915) treated *Flaveria* and *Sartwellia* as the only members of Flaveriinae in the traditional tribe Helenieae. *Haploësthes* was positioned by Rydberg (1927) in the Senecioneae (subtribe Senecioninae). Turner & Johnston (1961) proposed that *Haploësthes* is allied with the Flaveriinae, and maintained that the three genera belong together in Senecioneae rather than in the unnatural tribe Helenieae. Ornduff et al. (1963) have suggested that the inclusion of *Flaveria* and *Sartwellia* in Heliantheae (or Helenieae) is less taxing morphologically and cytologically than would be their inclusion with Senecioneae. A more detailed discussion of Flaveriinae and its tribal relationships is presented by Turner & Powell (1977), Nordenstam (1977), and Baagøe (1977). The present study offers little information regarding the tribal redisposition of the Flaveriinae, but hybridization data (see below) document the relationship of *Haploësthes* as proposed originally by Turner & Johnston (1961).

Morphology

In habit Flaverias vary from erect or spreading shrubs to robust or delicate annuals. In size some plants reach 4 m high (particularly *F. pringlei*), while the smallest individuals at ca. 6 cm may occur among populations of the desert annual taxa. Most of the species are rather stout herbaceous annuals or perennials which range from 0.5 to 2.5 m in height.

Branching stems and leaves are opposite and decussate in all species. The leaves are basally connate to weakly so in all taxa except *F. chloraefolia* where they are strikingly perfoliate. The plants typically are glabrous or microscopically pubescent except in *F. pubescens* where stems and leaves are covered rather densely with macroscopic hairs.

In capitulescence Flaverias are notable among the Asteraceae for their reduced and secondarily aggregated heads or synflorescences (Stuessy, 1976) in some species. The number of disc florets per head ranges from 1 to 15, with or without one ligulate ray floret. Synflorescences of maximum reduction are found in *F. trinervia* and *F. australasica* which have 1–2 floret heads clustered in axillary glomerules. Two major phyletic lineages are seemingly marked by number of phyllaries per head, one line with 5–6 phyllaries and the other with 3–4 phyllaries. Derived annuals may have fewer phyllaries per head.

The achenes of all Flaverias are black, ribbed, glabrous, and epappose except in *F. chloraefolia* and *F. mcdougallii* which have small pappus scales. In general *Flaveria* is characterized by reduced floral features which are similar in most species. In fact, most species differ by few morphological traits. Most dependable in delimiting taxa are differences in distribution, habit, foliage, capitulescence, and presence or absence of ray florets.

PHENOLOGICAL AND BREEDING CONSIDERATIONS

Within broad latitudinal ranges the flowering periods of different *Flaveria* species are generally overlapping. The Florida species seem to reach peak flowering in the fall and early winter, but may flower earlier or later, as is the case for *F. brownii* along the Texas coast, the species of southern Mexico, and other taxa. The xerophytic species of the southwestern United States and northern Mexico may flower from spring through fall depending upon moisture. Under controlled conditions in the greenhouse, annual species were noted to flower at vegetative maturity any time during the year, but they seemed to display most vigor from mid-summer into the fall. Perennials from Florida, Texas, and central Mexico also flowered from mid-summer through the fall. *Flaveria pringlei* of southern Mexico and *F. pubescens* from San Luis Potosí did not flower until late fall or winter, in the style of short-day plants.

Four of the annual species, *F. australasica*, *F. trinervia*, *F. bidentis*, and *F. campestris*, are self-compatible. The other annuals, *F. anomala*, *F. ramosissima*, *F. palmeri*, and probably *F. intermedia*, are basically self-incompatible as are all the perennial taxa so far as known. Self-fertilization occasionally may be stimulated by rubbing heads together as was done in attempts to secure artificial hybrids. The out-crossing species exhibit insect-pollinated florets in small heads that are secondarily aggregated into clusters that evidently attract pollinators. In some species the heads are discoid, while in others at least a few heads per cluster contain one ray floret each with the ligule being prominent to inconspicuous. In several species, most spectacularly in *F. anomala*, the uniligulate heads have peripheral arrangement in the clusters, and thus display the effect of a typical radiate composite head.

The four self-compatible annuals show reduced morphological features that are suggestive of the trend toward self-fertilization (Ornduff, 1966). The capitulescences of these species are reduced, inconspicuous, axillary glomerulate clusters, particularly in *F. trinervia* and *F. australasica*, and surely are not as attractive to insects as are the flower arrangements of other species. Furthermore, the self-fertilizing annuals have tiny, nearly microscopic ligules, and exhibit a low number of florets per head (1–8), smaller disc florets, and a smaller number of pollen grains per anther.

The self-compatible Flaverias characteristically produce only one or rarely two viable achenes per head when grown under insect free conditions. The viable achenes usually are produced by perfect disc florets which in most species exhibit shorter fruits than those of the pistillate ray florets. However, when intentionally crossed, or under field conditions, complete complements of mature fruits per head are often produced. Under natural conditions, therefore, it is assumed that a dual breeding system of self- and cross-pollination is operative in producing both uniform and variable genotypes.

The self-compatible species of *Flaveria* have widespread distributions as compared to the relatively localized self-incompatible taxa. This situation has been noted in other plant groups (Stebbins, 1957) where self-pollinators tend to be successful colonizers under ecologically variable conditions. The self-

pollinating Flaverias are the only successful "weedy" species of the genus. I believe that the self-compatible species are derived, as suggested by specialized morphological features, annual habit, and breeding system (Stebbins, 1957; Ornduff, 1966).

Chromosomal Considerations

Chromosome numbers of $n = 18$ are known for 18 of the 21 species of *Flaveria* (Powell & Powell, 1977, 1978; Keil & Stuessy, 1977). The three taxa for which chromosome numbers are unknown are from Mexico: *F. angustifolia*, *F. intermedia*, and *F. vaginata*. *Flaveria* is consistently diploid, with two exceptions, and a base number of $x = 18$ seems certain for the genus. Anderson (1972) reported $n = 9$ for one collection of *F. campestris*, a species that otherwise is $n = 18$. Anderson concluded that the $n = 9$ was a case of polyhaploidy rather than a relict ancestral diploid, and I agree. Two collections of *F. pringlei* (*Dillon 681*; *Hartman et al. 3834*) were counted as $n = 36$, the only polyploids known for the genus or the subtribe; *F. pringlei* also is $n = 18$.

The related genera *Sartwellia*, with all four species counted, and *Haploësthes*, with five of six taxa counted, are uniformly $n = 18$ (Turner, 1971, 1975). Thus the base number of Flaveriinae seems well established as $x = 18$.

Hybridizations

All crosses were conducted in a greenhouse with plants grown from perennial bases, lower stem cuttings, or from seed. Crosses were attempted by rubbing heads together once or twice per day for two to four days until the styles had withered. Heads were bagged with thin plastic to prevent accidental pollination. Achenes usually matured in about two weeks, after which they were collected and stored at room temperature for one to several weeks before planting. Germination usually occurred in one or two weeks. Seedlings grew to flowering stages in one to several months.

Crossability estimates, pollen stainability (PS) percentages, and meiotic observations (Table 1) were obtained by procedures and techniques outlined in Powell (1972). In Table 1 absence in some cases of pollen stainability (PS) and meiotic observations signifies that no F_1 hybrids of the particular combination could be grown to maturity. Artificial crosses between self-sterile species, both closely and distantly related, were found in many instances to stimulate selfing. Crosses involving a self-compatible female parent (*F. australasica*, *F. bidentis*, *F. campestris*, or *F. trinervia*) often gave rise to a mixture of selfs and hybrids.

The recognition of hybrid as opposed to selfed progeny was sometimes difficult. Flaverias typically are reduced in vegetative and floral characters. While the species are easily recognized as distinct in their natural habitats, artificial hybrids between morphologically similar parents are often difficult to identify. Consequently, caution was always used in characterizing hybrid progeny. With certain combinations (e.g., *F. palmeri* × *F. anomala*) it was necessary to evaluate the low PS and asynaptic meiotic behavior (Table 1) before being sure the progeny were hybrids. In instances where PS and meiotic behavior failed to

TABLE 1. Artificial hybrids with crossability and indices of interfertility.

F_1 Hybrid combinations	Crossability	Pollen Stainability (%)	Meiotic Observations
	INTERSPECIFIC CROSSES (*Flaveria*)		
Flaveria anomala		97	
× *F. bidentis*	Zero[a]		
× *F. palmeri*	Low–medium	13	Highly asynaptic, 6–12 heteromorphic II, the remainder I
× *F. trinervia*	Zero[a]		
F. australasica		92	
× *F. bidentis*	Medium[b]		
× *F. linearis*	Low–high[c]	2	Highly asynaptic, 5–10 II or pseudoassociations, the remainder I
× *F. palmeri*	Medium	19	Seemingly regular, 18 II, but with slight II heteromorphism
× *F. trinervia*	High[c]		
F. bidentis		83	
× *F. anomala*	Medium[c]		
× *F. campestris*	Medium–high[c]	45	Mostly regular with 18 II; occasional cells with 17 II, 2 I
× *F. trinervia*	High[c]	62	
F. brownii		87	
× *F. anomala*	Very low		
× *F. floridana*	High	64	Seemingly regular, 18 II
× *F. oppositifolia*	High	36	Seemingly regular, 18 II; occasional pseudoassociations at diakinesis; occasional cells with 17 II, 2 I
F. campestris		87	
× *F. anomala*	Low		
× *F. bidentis*	Medium	49	Seemingly regular, 18 II, but with slight heteromorphic pairing; occasionally 17 II, 2 I; occasional laggards at anaphase I
× *F. palmeri*	Low–medium		
× *F. trinervia*	Medium		
F. chloraefolia		78	
× *F. linearis*	Medium		
× *F. mcdougallii*	Zero[a]		
× *F. pringlei* ($n = 36$)	Zero[a]		
× *F. trinervia*	Zero[a]		
F. floridana		61	
× *F. brownii*	High	47	Regular, 18 II; possibly with some slight II heteromorphism
× *F. linearis*	Medium–high	65	Regular, 18 II; occasionally 3–4 early separating II, or pseudoassociations
× *F. palmeri*	High	3	Irregular, 12–17 II, 12–2 I; occasionally appearing regular with 18 II; frequently pseudoassociations; frequent laggards at anaphase I
× *F. pringlei* ($n = 18$)	Zero[a]		
× *F. sonorensis*	Very low		
F. intermedia		96	

TABLE 1. (Continued)

F_1 Hybrid combinations	Crossability	Pollen Stainability (%)	Meiotic Observations
F. linearis		81	
× *F. australasica*	Very low	11	Irregular, 13–18 II, 10–0 I; frequent laggards at anaphase I; heteromorphic II
× *F. chloraefolia*	Very low	33	Regular, 18 II; rarely 17 II, 2 I
× *F. floridana*	Medium–high	65	Regular, 18 II; possible pseudoassociations
× *F. mcdougallii*	Zero[a]		
× *F. oppositifolia*	High	19	Mostly regular, 18 II; occasionally early separating II; some lagging at anaphase I
× *F. palmeri*	High	12	Irregular, 14–17 II, 8–2 I; obvious II heteromorphism and pseudoassociations; 1–4 laggards common
× *F. pubescens*	Medium		
F. mcdougallii		80	
× *F. chloraefolia*	Zero[a]		
× *F. linearis*	Zero[a]		
× *F. oppositifolia*	Zero[a]		
F. oppositifolia		84	
× *F. anomala*	Zero[a]		
× *F. brownii*	Low–medium	54	Mostly regular, 18 II, or with 2–4 I and heteromorphic II; occasionally 1–4 laggards
× *F. linearis*	High	8	Regular, 18 II; rarely 17 II, 2 I
× *F. mcdougallii*	Zero[a]		
× *F. pringlei* ($n = 18$)	Zero[a]		
× *F. pubescens*	Low–high	81	Mostly regular, 18 II, less often 13–17 II, 10–2 I
× *F. sonorensis*	Zero[a]		
F. palmeri		99	
× *F. anomala*	Zero–medium[a]	22	Highly asynaptic, 7–16 II, obviously heteromorphic, the remainder I
× *F. australasica*	Zero[a]		
× *F. campestris*	Zero–low[c]		Regular, 18 II
× *F. linearis*	Very low	11	Highly irregular, 13–18 II, 10–0 I; anaphase I lagging and unequal segregation; occasional anaphase I bridges
F. pringlei ($n = 18$)		96	
× *F. anomala*	Zero[a]		
× *F. chloraefolia*	Very low		
× *F. floridana*	Zero[a]		
× *F. oppositifolia*	Very low–zero		
F. pringlei ($n = 36$)		92	
× *F. pringlei* ($n = 18$)	Very low		
F. pubescens		95	
× *F. linearis*	Low		
× *F. oppositifolia*	Zero–medium	74	Mostly regular, 18 II; usually 2–3 slightly heteromorphic II

TABLE 1. (Continued)

F_1 Hybrid combinations	Crossability	Pollen Stainability (%)	Meiotic Observations
F. ramosissima		99	
× *F. anomala*	Zero–high	32	Seemingly regular, 18 II; slightly irregular, 16–17 II, 2–4 I; or irregular, 12–14 II, 12–8 I, pseudoassociations
× *F. palmeri*	Low	11	Mostly regular, 18 II; occasionally 2–4 I
F. sonorensis		74	
× *F. floridana*	Zero[a]		
× *F. oppositifolia*	Zero[a]		
F. trinervia		83	
× *F. anomala*	Medium[c]	35	Asynaptic, 12–13 II and the remainder I; pseudoassociations at diakinesis
× *F. bidentis*	High[c]	14	Seemingly regular, 18 II; occasional laggards
INTERSPECIFIC CROSSES (*Sartwellia*[d])			
Sartwellia flaveriae		87	
× *S. gypsophila*	Very high	52	Regular, 18 II; bivalents appear heteromorphic
S. gypsophila		99	
× *S. flaveriae*	Low–medium	40	Regular, 18 II
× *S. puberula*	Medium	76	Regular, 18 II
S. mexicana		88	
× *S. puberula*	Very high	92	Regular, 18 II
S. puberula			
× *S. mexicana*	Medium–very high	88	Regular, 18 II; rarely 1 early separating bivalent
INTERSPECIFIC AND INFRASPECIFIC CROSSES (*Haploësthes*[d])			
Haploësthes greggii var. *texana* (Ter.[e])		98	
× *H. greggii* var. *texana* (Grand.[e])	Very low		
H. greggii var. *texana* (Grand.[e])			
× *H. greggii* var. *texana* (Ter.[e])	Low–medium	64	Mostly regular, 18 II; in some cells 1–3 pseudoassociations or 2–6 unpaired chromosomes; slightly heteromorphic II present in some cells
H. greggii var. *texana* (Ter.[e])			
× *H. robusta*	Zero–medium		
H. robusta			
× *H. greggii* var. *texana* (N. Mex.[e])	Low–medium	22	Mostly regular, 18 II; heteromorphic II evident in some cells; occasionally 1–2 I
H. robusta			
× *H. greggii* var. *texana* (Grand.[e])	Medium	65	Seemingly regular, 18 II; in some cells 2–3 possible pseudoassociations

TABLE 1. (Continued)

F_1 Hybrid combinations	Crossability	Pollen Stainability (%)	Meiotic Observations
H. robusta × *H. greggii* var. *texana* (Ter.[e])	High	69	Mostly regular, 18 II; 2–4 unpaired chromosomes present in some cells; slightly heteromorphic II present in some cells
INTERGENERIC CROSSES			
Haploësthes robusta × *Sartwellia puberula*	Very low	6[f]	Highly irregular, 9–12 II or pseudobivalents, 18–12 I; rarely 16–18 heteromorphic pairs
Haploësthes greggii var. *texana* × *Flaveria mcdougallii*	Very low		
Sartwellia puberula × *Flaveria chloraefolia*	Medium	0[g]	Highly asynaptic, 36 I or 1 II, 34 I; numerous laggards; unequal anaphase I segregation; laggards common; micronuclei common
× *Flaveria mcdougallii*	Very low (1 achene)		
Sartwellia mexicana × *Flaveria mcdougallii*	Zero		

[a] Crosses attempted, resulting in no seed-set.
[b] Seed germination poor, seedlings did not survive.
[c] Crossability estimated from seed-set; probably results from selfing in the self-compatible species.
[d] All species self-incompatible.
[e] Abbreviations of localities as follows: Ter. = Terlingua, Texas; Grand. = Grandfalls, Texas; N. Mex. = New Mexico.
[f] Pollen grains of several sizes; most obviously malformed.
[g] Three hybrid plants were grown to flowering stages; pollen was irregular in shape, obviously malformed.

indicate either selfing or hybridity, F_2 generation crosses often proved to be a convincing test in that F_2's could not be formed in most combinations (see below). Of course, hybrid progeny of crosses between species with clear morphological differences (e.g., rayed × discoid), and intergeneric crosses, were easily identified as such.

INTERSPECIFIC

Flaveria.—Artificial hybridizations were attempted with 16 species of *Flaveria* (Table 1). Interspecific F_1 hybrids were readily obtained from most combinations, even though the crossability of certain combinations did vary. Crossability was very low or zero (no viable seeds) in some combinations, but usually only zero crossability prevented the formation of experimental hybrids. Most F_1 hybrids were moderately to highly fertile as assessed from PS and meiotic behavior. Although PS (ranging from 2–99% in F_1 hybrids and parents; Table 1) must be viewed with caution (A. Jones, 1976), it may be useful in evaluating interfertility when compared with another criterion such as meiotic behavior.

Meiotic behavior in parental species is regular. In F_1 hybrids meiotic behavior varied from: regular, with seemingly normal bivalent formation; slightly irreg-

ular, with a few unpaired chromosomes, pseudoassociations, and/or heteromorphic bivalents; and highly irregular with numerous unpaired chromosomes in meiosis I configurations (Table 1). As expected, those combinations with grossly irregular meiosis were highly sterile. Multivalents were not observed in meiotic configurations of F_1 hybrids, suggesting an absence of translocations in the evolution of *Flaveria* species. The common observation of heteromorphic bivalents and pseudoassociations does suggest that small structural rearrangements and genic differences were involved with speciation. More drastic chromosomal and genic differences can be suspected where genomes of the interspecific hybrids are highly asynaptic.

Hybridizations were attempted between species that are relatively distantly related and between those that are presumably closely related, as judged from morphological and other characters. The experimental technique was not generally useful in assessing degrees of interspecific relationships in that the crossability and fertility data, themselves highly variable in F_1's, did not always correlate with seemingly obvious relationships. The F_1 hybrids of some distantly related species showed moderately high percentages of stainable pollen and quasi-regular meiosis, while the F_1's of more closely related species sometimes exhibited low PS and irregular meiosis. The interfertility measurements of some combinations corresponded with relationships which are suggested by morphology. Hybridization data with bearing on species relationships will be discussed in the taxonomic portions of this paper.

The ease with which wide-species crosses could be obtained was initially somewhat surprising. However, the same situation is true in *Perityle* (Powell, 1972), *Vernonia* (S. Jones, 1976), and other groups where the perennial taxa are exclusively allopatric and outcrossing, as they are in *Flaveria*. Perhaps reproductive barriers at the F_1 level are weak because they were not selected for in isolated populations. The strongest parental reproductive barriers in *Flaveria* are found to exist in the annual species. Several annual taxa occur sympatrically, even intermixed with other annual or perennial species, and yet I have not seen any evidence of natural hybridization. Perhaps this is because the annuals, which tend to have wider distributions, especially the weeds, are forced to develop reproductive barriers early in evolutionary divergence. Such evolutionary patterns have been noted among many other plant groups (Stebbins, 1950; Grant, 1971; Gadgil & Solbrig, 1972; Raven, 1976).

The true test of interspecific sterility in *Flaveria* is exhibited before or after the F_2 zygote level, at least under experimental conditions. Second or backcross generations were attempted with most of the F_1 combinations, but F_2's or backcrosses were obtained only with the following: *F. bidentis* × *F. campestris*; *F. bidentis* × *F. trinervia*; *F. brownii* × *F. floridana* (fertile); *F. campestris* × *F. bidentis*; *F. floridana* × *F. linearis*; *F. floridana* × *F. palmeri*; *F. linearis* × *F. chloraefolia*; *F. linearis* × *F. floridana* (fertile); *F. oppositifolia* × *F. brownii* (fertile); *F. oppositifolia* × *F. linearis*; *F. ramosissima* × *F. anomala*; *F. ramosissima* × *F. palmeri* (fertile); *F. trinervia* × *F. anomala*; *F. trinervia* × *F. bidentis*. All these crosses were sterile except for putative F_2's between the combinations indicated above as fertile. These exhibited moderate fertility based upon PS and

meiotic behavior. However, the species are so similar morphologically (and theoretically related) that it was not possible to be certain that the plants tested were indeed second generation hybrids. The F_1's of the above crosses were at least moderately fertile (Table 1). Further comments on the possible significance of the F_2's can be found in discussions of the species (see Taxonomy).

Sartwellia and Haploësthes.—Interspecific crosses were attempted also between the species of *Sartwellia* and *Haploësthes* (Table 1). All of the F_1 *Sartwellia* combinations showed relatively high crossability and fertility, suggesting that speciation in the genus might have been recent. Also, the Sartwellias are more homogeneous morphologically and ecologically than are the Flaverias (Turner, 1971; Powell & Turner, 1976). The species are perennial except for the annual S. *flaveriae*. One F_2 combination, S. *flaveriae* × S. *gypsophila*, was sterile, but not many F_2 crosses were attempted with the Sartwellias.

Both interspecific and infraspecific crosses were obtained with two of the three species of *Haploësthes*; material of *H. fruticosa* was not available (Turner, 1975). As was the case in *Sartwellia*, the interspecific combinations exhibited good crossability and interfertility. All the species are perennial. One backcross combination, *H. robusta* × *H. greggii* × *H. robusta*, was moderately fertile. Interestingly, the infraspecific hybrids seemed to be slightly less interfertile than did the interspecific crosses (Table 1), but this stage of investigation is still in progress.

Intergeneric

Crosses have been attempted between various species of *Flaveria*, *Sartwellia*, and *Haploësthes*, involving over 30 different intergeneric combinations. Thus far only two intergeneric crosses have been successful (Table 1). The remarkable artificial intergeneric hybrids are intermediate in morphology between the grossly different species involved, and they are absolutely sterile by all indications (Table 1).

The results of experimental hybridizations strongly support the generic integrity of *Flaveria*, *Sartwellia*, and *Haploësthes*. Interspecific F_1 hybrids are easily synthesized within each of the three genera. Intergeneric crosses are difficult to synthesize and sterile, thus clearly delimiting the genera by this experimental criterion. The genera also are clearly delimited morphologically. The experimental data support a relationship of *Haploësthes* with the Flaveriinae as proposed originally by Turner & Johnston (1961), through formation of the hybrid combination *Haploësthes robusta* × *Sartwellia flaveriae* (Table 1). The artificial intergeneric hybrid *Sartwellia puberula* × *Flaveria chloraefolia* supports a generic relationship that has long been accepted (Rydberg, 1915; Turner, 1971).

Experimental data (Table 1) have been useful in assessing the relationship of *Flaveria mcdougallii*, a recently described species from the Grand Canyon of Arizona (Theroux et al., 1977). The authors questioned the generic relationship of *F. mcdougallii* in that the new entity exhibits at least some features which are intermediate between or characteristic of both *Flaveria* and *Sartwellia*, but they assigned *F. mcdougallii* to the former genus based upon the preponderance

of data. Theroux et al. (1977) furthermore concluded that "If morphology alone were the deciding factor, the continued acceptance of *Flaveria* and *Sartwellia*, and possibly even *Haploësthes* as distinct genera might be questioned." Artificial crosses (Table 1) were attempted between *F. mcdougallii* and two species of *Sartwellia*, one species of *Haploësthes*, and three species of *Flaveria* in an effort to further evaluate the generic relationship of the new species. In all cases crossability was very low or zero, suggesting that *F. mcdougallii* is at least as isolated (or more so) from all three genera as they are from each other (Table 1). Although I agree with Theroux et al. (1977) that *F. mcdougallii* exhibits intermediate features, I do not believe that this obviously derived species bridges the morphological gap between three genera which are, in my opinion, both morphologically and biologically distinct. In fact, the experimental data thus far suggest that *F. mcdougallii* could be recognized as a monotypic genus (see Taxonomy).

NATURAL HYBRIDIZATION

Long & Rhamstine (1968) have reported evidence for the origin of *F.* × *latifolia* in Florida as a result of natural interspecific hybridization between *F. floridana* and *F. linearis*. They did not test the hypothesis experimentally because they were unable to grow the suspected parents in the greenhouse or garden. Both *F. floridana* and *F. linearis* have grown vigorously in the SRSU greenhouse, and F_1 interspecific hybrids are readily formed (Table 1). Furthermore, the *F. floridana* × *F. linearis* combination (and reciprocal) has given rise to seemingly fertile F_2 hybrids.

The interfertility of *F. linearis* × *F. floridana* supports the possibility of hybrid origin for *F.* × *latifolia* as concluded by Long & Rhamstine (1968). However, I have not been able to recognize *F.* × *latifolia* as a distinct taxon among collections from Florida. In fact, observations lead me to believe that *F. floridana* and *F. linearis* are spatially and ecologically isolated, or nearly so. If the two species do undergo natural hybridization, it is likely of sporadic occurrence, and the hybrids do not represent a populational entity in the sense of a species as proposed by Long and Rhamstine. At any rate, the morphological similarity of the two species causes difficulty in the positive recognition of experimental F_1 or F_2 hybrids.

Natural hybridization as a general phenomenon in *Flaveria* appears to be precluded by internal reproductive barriers and/or spatial isolation. Generally speaking any introgression would seem to be prevented by F_1 or F_2 sterility or by geographic isolation, except perhaps in *F. floridana* × *F. linearis*. The perennial species of *Flaveria* are all isolated geographically, with the possible exception of *F. floridana* and *F. linearis*, and some of the species in Puebla-Oaxaca, Mexico (see Taxonomy). The weedy annual species which may exist sympatrically exhibit the strongest internal reproductive isolation. I have not observed any indication of natural hybridization in *Flaveria* either from field investigations or from examination of exsiccatae, with the possible exception of *F. floridana* and *F. linearis*.

Chemical Considerations

A preliminary flavonoid analysis of the Flaveriinae was published by Al-Khubaizi (1977) who found that ca. 85% of the total flavonoids in this group are sulfated. Eleven species were examined: *Flaveria anomala*, *F. brownii*, *F. campestris*, *F. chloraefolia*, *F. palmeri*, *F. pringlei*, and *F. trinervia*; *Sartwellia flaveriae* and S. *puberula*; *Haploësthes greggii* var. *texana* and *H. robusta*. Among all the taxa, 65 components (spots) were detected chromatographically, and structural determination was realized for 17 compounds; 13 sulfated and 4 non-sulfated. Thirteen of the identified flavonoids were previously unknown.

Al-Khubaizi found that the negatively charged sulfated flavonoids may be mono-, di-, or tri-sulfated, and based upon skeletons of kaempferol, quercetin, isorhamnetin, patuletin, or spinacetin. Also the sulfates may be attached directly to the flavonoid skeleton or to a sugar (in glycosides).

At the time Al-Khubaizi (1977) began her study, sulfated flavonoids were poorly known, difficult to isolate, and difficult to characterize for structure. Consequently, much of the preliminary work by Al-Khubaizi involved the elucidation of techniques for working with sulfated flavonoids. Her success in elaborating several new techniques, including separation by paper electrophoresis and structure identification by UV spectral methods (not previously applied successfully in the study of sulfated flavonoids), should provide a basis for further investigations.

Perhaps the major systematic value of the preliminary flavonoid data is that they support the subtribal relationship of *Flaveria*, *Sartwellia*, and *Haploësthes*. The three genera have in common many of the sulfated flavonoids and an array of the more common flavone and flavonol aglycones and glycosides. Interspecific relationships in *Flaveria* and the other genera can not yet be evaluated on the basis of flavonoid chemistry until more compounds are known for more species.

Sulfated flavonoids are now known to occur in a broad spectrum of both monocot and dicot taxa (Al-Khubaizi, 1977). Whether or not the ability to synthesize sulfated flavonoids is the result of environmental adaptation is still open to question. Plants inhabiting saline, gypseous, or marshy areas tend to produce sulfated flavonoids. The latter is certainly true in the Flaveriinae where many species occur in saline or gypseous substrates. But in a broader survey of plant species in various habitats, Molly Whalen (pers. comm.) has found that plants in a wide variety of habitats may produce sulfated flavonoids. Thus an adaptive role for sulfated flavonoids remains to be shown.

Future flavonoid investigations in *Flaveria* (and related genera) should involve an attempt to identify the major compounds of all the species so that interspecific and intergeneric comparisons can be made. Furthermore, any adaptive correlation between flavonoid complements and C_4 or C_3 metabolism can be investigated when more data are available.

Kranz Syndrome and C_4 Metabolism

Smith & Turner (1975) discovered the Kranz syndrome and C_4 photosynthetic metabolism in *Flaveria* during their survey of the Asteraceae for this physiological

TABLE 2. Species of *Flaveria* with C_3 and C_4 photosynthetic metabolism, as determined by C^{12}/C^{13} ratios (Walter Brown, pers. comm.).

C_3 Species	C_4 Species
1. *F. angustifolia*	1. *F. australasica*
2. *F. anomala*	2. *F. bidentis*
3. *F. chloraefolia*	3. *F. brownii*
4. *F. floridana*	4. *F. campestris*
5. *F. linearis*	5. *F. cronquistii*
6. *F. mcdougallii*	6. *F. intermedia*
7. *F. oppositifolia*	7. *F. palmeri*
8. *F. pringlei*	8. *F. trinervia*
9. *F. pubescens*	9. *F. vaginata*
10. *F. ramosissima*	
11. *F. robusta*	
12. *F. sonorensis*	

trait. In Asteraceae they found C_4 metabolism to occur in five small genera of subtribe Coreopsidinae (Heliantheae), in all members of the genus *Pectis* (Tageteae), and in four species of *Flaveria*. According to the above survey, *Flaveria* is unique in Asteraceae in that both C_3 and C_4 species occur in the same genus. Both *Sartwellia* and *Haploësthes* are characterized by C_3 species (W. V. Brown, pers. comm.).

Additional studies of the Kranz syndrome in *Flaveria* (W. V. Brown, pers. comm.) revealed five other C_4 species for a total of nine in the genus (Table 2). Furthermore, through leaf anatomical studies of most *Flaveria* species, Brown (pers. comm.) has concluded that certain species (e.g., *F. oppositifolia*, *F. linearis*, *F. floridana*) are intermediate between non-Kranz and Kranz anatomy. According to Brown, *Flaveria* is unique in having the intermediate species. Other genera that contain both non-Kranz and Kranz species do not have intermediates, except possibly the single species *Euphorbia acuta*. Thus some of the Flaverias seem to be in the process of evolution from non-Kranz to Kranz physiology.

In angiosperms C_4 metabolism is a fairly widespread, derived process, perhaps having several independent origins (Björkman & Berry, 1973; Smith & Brown, 1973; Kennedy & Laetsch, 1974; Brown, 1977). The Kranz syndrome also is derived in *Flaveria*, occurring mostly in the advanced annual species. If my phylogenetic speculation is correct (see below), C_4 metabolism has evolved twice in *Flaveria*.

Björkman & Berry (1973) emphasize the adaptive significance of C_4 metabolism in arid land plants. The annual C_4 species of *Flaveria* certainly thrive under arid conditions, although possibly under mesic conditions as well. *Flaveria brownii*, a weak perennial C_4 species, occupies mesic-saline habitats along the Texas Gulf Coast. The C_3 species of *Flaveria* also exist under both xeric and mesic conditions. Since both C_3 and C_4 species of *Flaveria* thrive in relatively arid and saline habitats, it does not seem likely that C_4 taxa evolved in selective response to these stringent environmental factors alone. Instead, I suspect that the adventitious annuals found C_4 metabolism to be advantageous in occupying

a wide variety of habitats, including those dry and salty. *Flaveria brownii* also appears to be a derived and geographically dispersed species (see Taxonomy).

Evolutionary Considerations

The present distributional center for Flaveriinae is in the general Chihuahuan Desert region (Turner, 1971, 1975; present paper). All the species of both *Sartwellia* and *Haploësthes* are located within this region, as are many species of *Flaveria*, while several perennial species of *Flaveria* are distributed elsewhere in Mexico, Texas, and Florida.

Current distribution suggests that the Flaveriinae might have originated in the north central highlands of Mexico, and the centralization of Flaveriinae in the Chihuahuan Desert suggests that evolution of the group might have been correlated with formation of the desert in the Pliocene or Pleistocene (Axelrod, 1948; Sharp, 1953). The Flaveriinae could have evolved rapidly in response to Pleistocene climatic fluctuations, extending from mesic habitats into increasingly xeric and saline surroundings.

Of the three genera in Flaveriinae, *Haploësthes* (Turner, 1975) seems to possess the most ancestral traits, including larger heads, 5–8 ray florets, pappus of 25–40 setose bristles, and pubescent achenes (with scattered 2-celled hairs). *Sartwellia* (Turner, 1971) has smaller heads, five ray florets with reduced ligules, pappus of scales and bristles, and pubescent achenes. *Flaveria* is uniformly reduced in terms of these characters, having small heads with 1–15 florets, heads discoid or with one ray floret, pappus absent (except squamellate in two species), and glabrous achenes. *Flaveria* is by far the most successful genus in the Flaveriinae, with its 21 species, as compared with the 4 species of *Sartwellia* and 3 species of *Haploësthes*. *Flaveria* and *Sartwellia* clearly are closest in terms of intergeneric relationships, while *Haploësthes* does not seem as closely related to either of the former genera (although close enough to *Sartwellia* for rare artificial crosses). It is largely through *Haploësthes* that the Flaveriinae are related to Senecioneae (Turner & Powell, 1977) although the tribal relationships of Flaveriinae, like many Helenieae, are obfuscated by reduction and loss of characters.

The genus *Flaveria* with more, morphologically diverse species has a wider distribution (see Taxonomy) than the other two genera of the subtribe. However, only the derived annual species are widespread in South America, Africa, Australia, and the central United States. The perennial, supposedly more primitive taxa are located in Mexico. In my opinion the most primitive-looking Flaverias are to be found among the four species centered in the Tehuacán Valley of Puebla-Oaxaca, e.g., *F. angustifolia* and *F. vaginata*. These are somewhat woody shrubs or small trees to 3–4 m high, with large, thick leaves, and numerous, rather thick, radiate heads. *Flaveria chloraefolia* of the Chihuahuan Desert region also exhibits ancestral traits in its mesic-marshy habitat, large semisucculent habit, large perfoliate leaves, and large heads. Therefore, in terms of broader distribution and primitive habit, *Flaveria* could be considered ancestral in the Flaveriinae.

A phylogenetic scheme of *Flaveria* based upon morphological, experimental,

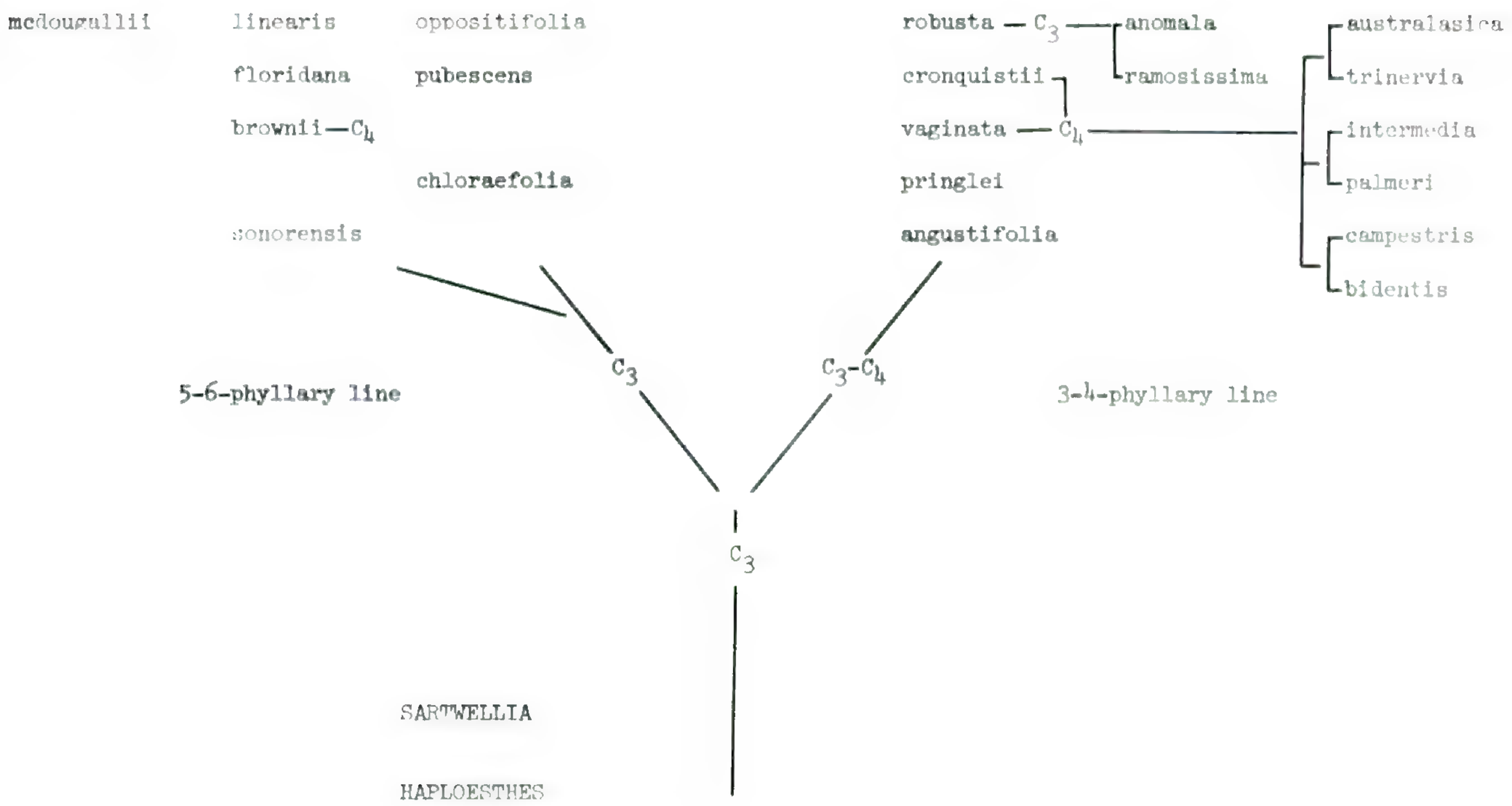

FIGURE 1. Phylogenetic arrangement of *Flaveria*, showing subgeneric groups informally designated as the 5–6-phyllary line and the 3–4-phyllary line. Groupings and brackets indicate suspected relationships; species and lineages with C_4 metabolism are indicated. *Sartwellia* and *Haploësthes* are the other two genera of Flaveriinae, both exhibiting more ancestral traits than *Flaveria*.

chemical, and eco-geographic considerations is presented in Fig. 1. There are two major lineages as indicated by the perennial group with 3–4 phyllaries and the group with 5–6 phyllaries, and the two phyletic lines occur in separate major centers of distribution. The species with 3–4 phyllaries are centered in Puebla-Oaxaca with one species, *F. robusta*, in Colima. The taxa with 5–6 phyllaries have a much wider distribution in central and northern Mexico. The large, shrubby species of the semiarid Tehuacán Valley and vicinity in Puebla-Oaxaca exhibit several ancestral traits, and it is tempting to hypothesize the origin of *Flaveria* from the Puebla-Oaxaca region with the northern species proliferating from this center. However, it is difficult to envision derivation of the line with 5–6 phyllaries directly from the Puebla-Oaxaca species. Both *Sartwellia* and *Haploësthes* have involucres with 5–6 phyllaries, thus supporting an ancestral position of the 5–6-phyllary line in *Flaveria*. *Flaveria oppositifolia* and *F. chloraefolia* have the widest distributions of the northern species. Populatons of *F. oppositifolia* from Zacatecas and San Luis Potosí and the localized *F. pubescens* of San Luis Potosí with wider, perfoliate leaves represent my idea of primitiveness in the 5–6-phyllary line, except that their rather large, numerous heads are discoid. Perhaps the two major lineages of *Flaveria* originated somewhere between the two present distributional centers, with conditions of increasing aridity enhancing the proliferation of each line. The Puebla-Oaxaca species have remained environmentally more restricted than the northern Chihuahuan Desert species.

The eight annual species seem obviously derived from one or more of the

perennial groups as suggested in Fig. 1. All the annuals are radiate, and thus it appears that their origin is from one or more of the groups with radiate species. Although the annuals exhibit many reduced traits, they seem to be most like the *F. angustifolia* group in phyllary shape and number, and in capitulescence, but more like the *F. linearis* group in leaf shape and texture. The close relationship indicated for *F. anomala* and *F. ramosissima* in Fig. 1 requires additional study. All of the other annual species appear related morphologically, and all exhibit C_4 physiology (Fig. 1). All the C_4 annuals are self-compatible, except for *F. palmeri* and probably *F. intermedia*.

Speciation in *Flaveria* (and Flaveriinae), especially with the perennial species, would appear to have followed geographic isolation. Among annual species, both geographic speciation and that resulting from internal reproductive barriers seems to have occurred (Table 1).

Important evolutionary trends in the Flaveriinae include the formation of sulfated flavonoids, theoretically as an adaptation to gypseous and saline habitats, and the development of efficient C_4 metabolism in some annual and perennial taxa. The C_4 metabolism is best developed in the 3–4-phyllary line, but seems to have evolved at least twice in *Flaveria*, occurring also in one species (*F. brownii*) of the 5–6-phyllary line (Fig. 1). There is a trend toward more facultative genotypes such as those exhibiting annual habit, C_4 metabolism, and self-compatibility. The wide distribution of *F. linearis* also attests to its facultative nature even though it is C_3, self-incompatible, and perennial.

Additional discussions of species relationships, including evidence upon which such judgments are based, are included in Taxonomy.

Taxonomy

Flaveria Juss., Gen. Pl. 186. 1789; J. F. Gmel., Syst. Nat. 2: 1269. 1791. LECTOTYPE: (Johnston, 1903).

Vermifuga R. & P., Prodr. Fl. Per. 114. 1794.
Brotera Spreng., J. Bot. (Schrader) 1800: 189, *pl.* 5. 1801, non *Brotera* Cass. 1799.
Nauenbergia Willd., Sp. Pl. 3: 2393. 1804.

Plants delicate or vigorous annuals or perennials, 5–200 cm high, in some species small trees to 4 m high, stems numerous or few, opposite and decussate, erect, lax, or decumbent, often purplish, glaucous, glabrous to densely short-pubescent, often merely tufted-pubescent in the axils. Leaves opposite and decussate, petiolate or sessile, often barely connate, less often connate or connate-perfoliate, 2–15 cm long, 0.2–5 cm wide, glabrous or short-pubescent, linear, lanceolate, oblong-ovate, ovate, elliptic, oblanceolate, the margins entire, serrate or weakly so, serrate-dentate, or spinulose-serrate; in many species, persistent sheathing bases of fallen leaves ringing the stems. Capitulescences of tightly or loosely aggregated heads on short peduncles in usually flat-topped corymbose panicles, or glomerulelike synflorescences in axils; heads radiate or discoid, if both are present then usually discoid heads central and radiate heads peripheral; receptacles small, convex, naked, or setose in 2 species; involucres 2.5–7 mm long, subcylindrical or angular, oblong or suburceolate, the phyllaries 2–5, concave or

boat shaped, becoming swollen and corky in one species, ovate, lanceolate, or oblong, the apices rounded, acute, lacerate, or beaked; calyculate bracts linear-lanceolate. Ray florets 1 (rarely 2) when present, pistillate and fertile, the ligules yellow, cream yellow in *F. trinervia*, oblong, ovate or elliptic, usually rather small and inconspicuous; disc florets 1–15, the corollas yellow, 2–4 mm long, prominent tubes naked or minutely-pubescent, the throats gradually or abruptly expanded, narrowly funnelform to campanulate, usually with multicellular hairs, the lobes 5, short, acute, the styles less than 1 mm long, linear-oblong, flattened, obtuse and minutely pubescent at the apices, the anthers 1–2 mm long, with conic appendages. Achenes black, 10-ribbed, somewhat flattened, glabrous, 1–3.6 mm long, those of the ray florets usually larger and somewhat longer than those of the disc florets, narrowly oblanceolate or linear-oblong; pappus absent, or in one species of 2–4 unequal, hyaline, incurved squamellae, 0.5–1 mm long, or in another species a low crown of united scales. Base chromosome number, $x = 18$.

Type species: *Flaveria chilensis* J. F. Gmel. = *F. bidentis* (L.) Kuntze.

a. Pappus scales present.
  b. Leaves perfoliate, to 4–5 cm wide; Chihuahuan Desert region ..... 1. *F. chloraefolia*
  bb. Leaves weakly connate, to 0.7 cm wide; Arizona ..... 21. *F. mcdougallii*
aa. Pappus absent.
  c. Receptacle of glomerule setose.
    d. Achenes 2–2.6 mm long; plants widespread in North America and elsewhere. ..... 15. *F. trinervia*
    dd. Achenes 2.3–4.5 mm long; plants of Australia ..... 16. *F. australasica*
  cc. Receptacle naked.
    e. Plants annual.
      f. Heads tightly clustered in glomerules.
        g. Ligules ca. 1 mm or less; South America to Florida, Africa, lower Europe ..... 13. *F. bidentis*
        gg. Ligules 1.5–2.5 mm long; New Mexico and Texas north to Colorado to Kansas ..... 14. *F. campestris*
      ff. Heads loosely clustered.
        h. Ligules 2 mm long or less.
          i. Throat of disc corolla narrowly funnelform; Coahuila ..... 17. *F. palmeri*
          ii. Throat of disc corolla expanded to broadly funnelform or campanulate; Durango ..... 18. *F. intermedia*
        hh. Ligules 3 mm or longer.
          j. Disc florets 1–2(–3); achenes 1.3–2.2 mm long; Coahuila, Nuevo León, Tampico, Mexico ..... 19. *F. anomala*
          jj. Disc florets 5–8(–10); achenes ca. 1 mm long; Oaxaca, Puebla ..... 20. *F. ramosissima*
    ee. Plants perennial.
      k. Phyllaries 3–4; southern Mexico, Puebla-Oaxaca to Colima.
        l. Ligules absent.
          m. Heads rather densely aggregated ..... 9. *F. pringlei*
          mm. Heads rather loosely arranged in flat-topped panicles ..... 11. *F. cronquistii*
        ll. Ligules present.
          n. Upper herbage densely short pubescent ..... 10. *F. vaginata*
          nn. Upper herbage glabrous or essentially so.
            o. Florets 5–7; south-central Mexico ..... 8. *F. angustifolia*
            oo. Florets 3; Colima, adjacent Michoacán ..... 12. *F. robusta*
      kk. Phyllaries usually 5 or more.
        p. Ligules absent.

q. Plants densely pubescent ..... 2. *F. pubescens*
qq. Plants essentially glabrous, less often moderately pubescent ..... 3. *F. oppositifolia*

pp. Ligules present.
r. Disc florets 10–15, sometimes as few as 5 in *F. brownii*.
s. Disc florets 5–10; plants of the Texas Gulf Coast ..... 4. *F. brownii*
ss. Disc florets 9–14; plants of the Florida west coast, especially Tampa and vicinity south ..... 5. *F. floridana*
rr. Disc florets usually 5–8.
t. Phyllaries 5(–6), linear or oblong; plants of Florida, Bahamas, Cuba, Yucatán, Quintana Roo ..... 6. *F. linearis*
tt. Phyllaries (4–)5, linear; plants of the Río Mayo region, Sonora ..... 7. *F. sonorensis*

In accounts of the following species, lists of Representative Specimens were selected from more extensive collections of the taxa concerned, while distribution maps were made from complete locality data. Label data are available at SRSU for all specimens of *Flaveria* examined during the study.

1. **Flaveria chloraefolia** A. Gray, Mem. Amer. Acad. Arts, n.s., 4: 88. 1849. TYPE: Mexico, Chihuahua (Durango?), Pelayo, NW of Mapimi, May, *Wislizenus 274*? (GH, holotype, not seen; MO, isotype).

Plants perennial, the stems erect to subdecumbent, 0.3–2 m long, glaucous, often purplish; leaves opposite, connate-perfoliate, 3–10 cm long, 1–4(–5) cm wide, glaucous, often purplish, oblong-ovate to lanceolate or hastate, the margins entire; capitulescence of numerous heads loosely to tightly aggregated into large, paniculate corymbs; heads discoid; involucres 6–7 mm long, oblong-urceolate, the phyllaries 5; calyculate bracts ca. 2 mm long; disc florets 9–13, the corollas ca. 4 mm long, the tube 1.2–1.4 mm long, the throat ca. 2 mm long, narrowly funnelform, the lobes ca. 0.5 mm long, acute; styles ca. 1 mm long, truncate-puberulent; anthers ca. 2 mm long; achenes 2.5–3 mm long, slightly dimorphic in length, narrowly oblanceolate to linear; pappus of 2(–4) unequal, hyaline scales, 0.5–1 mm long, usually on one shoulder, rarely absent; chromosome number, $n = 18$.

Widely distributed in the northern Chihuahuan Desert region, extending up the Pecos River drainage into central New Mexico, probably extending up the Rio Grande to north of Las Cruces, and south to central Coahuila, Mexico (Fig. 2); associated with permanent or ephemeral saline water sources such as marshes, springs, creeks, rivers, irrigation canals, or roadside ditches. Flowering usually in late summer or fall.

REPRESENTATIVE SPECIMENS: MEXICO. CHIHUAHUA: 2 mi NW of Meoqui, *Cronquist 10232* (CAS, GH, KSC, MICH, NY, TEX, US, WIS). COAHUILA: Hermanas, *Marsh 1635* (F, GH, SRSU, TEX). Near Parras and San Lorenzo, *Palmer 2083* (GH). 100 mi N of Monclova, Sabinas River, *Palmer 682* (GH, MO, NY, US). 6 mi SW of Cuatro Ciénegas, *Powell & Tomb 2622* (TEX, US). 12 mi E of Cuatro Ciénegas, *Powell & Turner 2278* (TEX).

UNITED STATES. NEW MEXICO: Chaves Co., 0.5 mi SW of Frazier, *Waterfall 6175* (GH, MO, NY). Guadalupe Co., Santa Rosa, *Crutchfield 2320* (LL). TEXAS: Culberson Co., 12 mi W of Orla, *Correll & Correll 24688* (LL). Pecos Co., Ft. Stockton, *Wooton s.n.* (US). Reeves Co., ca. 0.5 mi E of Toyahvale, *Powell 2799* (TEX, US). Terrell Co., Independence Creek, *Warnock & Johnston 17281* (SRSU).

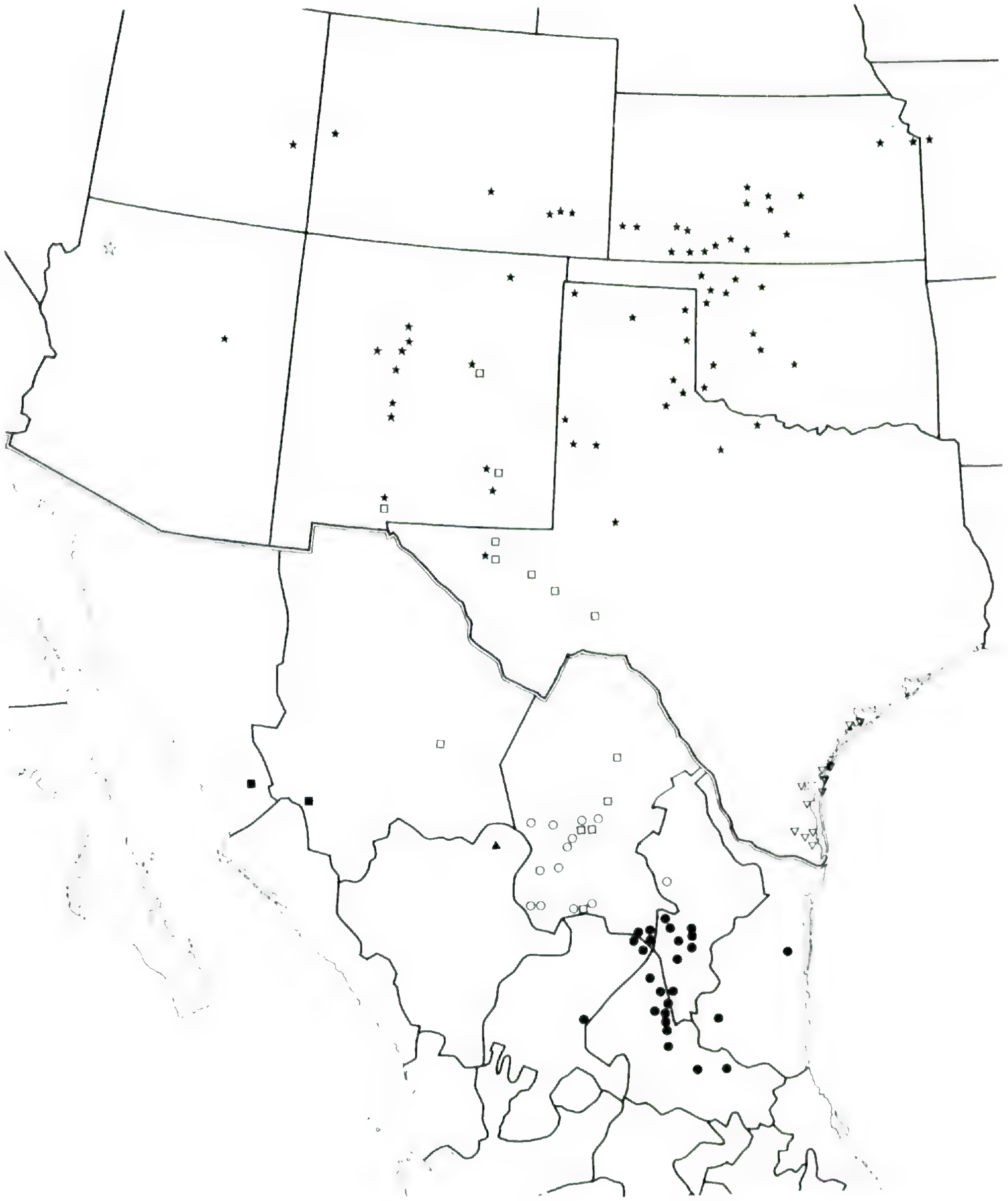

FIGURE 2. Distribution of *Flaveria chloraefolia* (open squares); *F. campestris* (closed stars); *F. palmeri* (open circles); *F. anomala* (closed circles); *F. sonorensis* (closed squares); *F. mcdougallii* (open star); *F. intermedia* (closed triangle); *F. brownii* (open triangles).

Flaveria chloraefolia is one of the most distinctive species of the genus with its rather succulent habit, perfoliate leaves, large flat-topped clusters of discoid heads, and 2–4 pappus scales. The taxon is not closely related to any other *Flaveria*, and could be considered primitive (Fig. 1) on the basis of its habit, leaves, and pappus scales. *Flaveria chloraefolia* does show some alliance with *F. oppositifolia* and *F. pubescens* with their large discoid heads and basally

connate leaves in some populations. Interestingly the species did cross and form hybrids with *F. linearis* (Table 1), which would appear distantly related, and it did form an intergeneric hybrid with *Sartwellia puberula*, which has little in common morphologically except the pappus scales.

2. **Flaveria pubescens** Rydb., N. Amer. Fl. 34: 145. 1915. TYPE: Mexico, San Luis Potosí, Río Verde, 2–8 June 1904, *E. Palmer 26* (NY, holotype; F, GH, K, MO, NY, isotypes).

F. longifolia A. Gray var. *subtomentosa* Greenman & Thompson, Ann. Missouri Bot. Gard. 1: 413. 1915, pro parte. TYPE: Mexico, Río Verde, 17 Nov. 1910, *C. R. Orcutt 5421* (MO, holotype).

Plants stout perennials, 30–80 cm high, the stems erect, densely short-pubescent; leaves opposite, connate, 5–10 cm long, 0.4–1.2 cm wide, densly short-pubescent, linear, the margins entire; capitulescence of numerous heads rather tightly aggregated in flat-topped, rather loose, corymbose panicles; heads discoid; involucres ca. 4 mm long, the phyllaries 5, linear-oblong; disc florets 10–15, the corollas 2.8–3.3 mm long, the throats funnelform; achenes 1–1.7 mm long, oblanceolate or linear; pappus absent; chromosome number, $n = 18$.

Scattered localities, possibly in gypsum soils, San Luis Potosí and Tamaulipas, Mexico (Fig. 3).

REPRESENTATIVE SPECIMENS: MEXICO. SAN LUIS POTOSÍ: 1 mi SE of Río Verde, *Hartman et al. 3823* (LL). Minas de San Rafael, *Purpus 4776* (F, GH, UC, US). TAMAULIPAS: Jaumave Valley, *Nelson 4450* (F, GH, US).

Flaveria pubescens is closely related to *F. oppositifolia* which is perhaps of recent divergence. There is essentially no difference in floral characters of the two taxa, but *F. pubescens* is distinguished by the densely pubescent herbage and usually much broader, linear leaves which are connate-perfoliate. *Flaveria oppositifolia* is more widely distributed than is *F. pubescens* (Fig. 3), and the leaves are usually narrow, but in a few populations the leaves are wider and the plants are somewhat pubescent. It would be possible to regard *F. pubescens* and *F. oppositifolia* as varieties of one species. The crossability and interfertility of the two taxa are variable and fairly high (Table 1), but interfertility is not any greater than between some quite distinct species of the genus. I have maintained the two species primarily because they are morphologically distinguishable.

3. **Flaveria oppositifolia** (DC.) Rydb., N. Amer. Fl. 34: 146. 1915. TYPE: Mexico, Tamaulipas, between San Fernando and Santander, Oct. 1930, *Berlandier 2263* (=*843*), (GH, lectotype; K, MO, NY (2), isolectotypes).

Gymnosperma oppositifolium DC., Prodr. 5: 312. 1836.
Flaveria longifolia A. Gray, Mem. Amer. Acad. Arts, n.s., 4: 88. 1849. TYPE: Mexico, Coahuila, near Ciénega Grande, May, *Gregg s.n.* (GH, holotype; MO, isotype).

Plants stout perennials, 30–80 cm high, the stems erect, sometimes purplish, glabrous, essentially so, or short-pubescent; leaves opposite, sessile, rarely barely connate, 3.5–12 cm long, 0.2–0.9(–1.2) cm wide, glabrous, essentially so, or short-

Figure 3. Distribution of *Flaveria angustifolia* (closed triangles); *F. pringlei* (closed circles); *F. vaginata* (open squares); *F. cronquistii* (open triangles); *F. robusta* (closed squares); *F. oppositifolia* (open circles); *F. pubescens* (open stars); *F. ramosissima* (closed stars).

pubescent, linear, tapering from the sessile base, the margins entire or weakly spinulose-serrate; capitulescense of numerous heads rather tightly aggregated in flat-topped, rather loose, corymbose panicles; heads discoid; involucres 4–4.7 mm long, the phyllaries 5, linear-oblong, acute or rounded apically; calyculate bracts 1–2, linear, 1–2 mm long; disc florets 9–13(–15), the corollas 2.8–3 mm long, the tubes ca. 1.2 mm long, the throats 1.2–1.5 mm long, narrowly funnelform to broadly so, may be abruptly expanded in the distal half, the lobes ca.

1 mm long, acute; anthers ca. 1.5 mm long; achenes 1.5–1.8 mm long, oblanceolate or linear; pappus absent; chromosome number, $n = 18$.

Scattered populations, high gypsum plains or other areas with dilute gypsum, saline, or rarely loamy soil, usually in moist areas or in disturbed habitats at roadside, 1,450–2,340 m, northeast-central Mexico (Fig. 3).

REPRESENTATIVE SPECIMENS: MEXICO. AGUASCALIENTES: near Ciénega Grande, *McVaugh 23783* (DS, MICH). COAHUILA: Hermanas, *Marsh 1643* (GH, SRSU, TEX). Saltillo and vicinity, *Palmer 304* (ARIZ, F, GH, MO, NY, UC, US). 6 mi W of Nadadores, *Powell & Turner 2266* (TEX). 2 mi N of Parras, *Ward 5750* (MICH). 44 mi SW of Monterrey, *Warnock & Barkely 14765M* (F, TEX, US). DURANGO: 9 mi N of Dgo.-Zac. border, *Sikes et al. 831* (TEX, US). HIDALGO: near Tula, *Graham & Johnston 4024A* (MICH, TEX). NUEVO LEÓN: Galeana, *Chase 7636* (ARIZ, F, GH, MICH, NY). 45 mi SE of Saltillo, *Powell & Tomb 2561* (TEX, US). SAN LUIS POTOSÍ: 2 mi S of Cedral, *Johnston 7582* (GH, US). Hacienda de Angostura, *Pringle 3767* (CAS, G, GH, LL, MICH, MO, NY, TEX, UC, US). 6 km NE of Matehuala, *Rzedowski 4873* (TEX). TAMAULIPAS: Jaumave, *Berlandier 3173* (GH, K, MO, NY, US). ZACATECAS: 55 mi NE of Jnct. 49-54, *Powell & Tomb 2593* (TEX, US). Sierra Hermosa, *Shreve 8593* (ARIZ, CAS, US).

There are several species that occur within the same distributional range as *F. oppositifolia* (Figs. 2–3), but the latter taxon is readily distinguished by its perennial habit, linear, mostly glabrous leaves, capitulescene of numerous discoid heads rather loosely aggregated in flat-topped clusters, 5 phyllaries, and 9–15 florets per head. *Flaveria oppositifolia* is closely related to *F. pubescens* which has densely pubescent herbage.

Plants from separate populations of the wide-ranging *F. oppositifolia* do show notable variation in certain features, particularly in habit, leaf size, and pubescence, but this variation is without apparent taxonomic significance. Plants of the higher elevation gypsum plains are usually stiffly erect whereas those plants from near Monclova at lower elevations are usually lower and more reflexed in habit. Leaf width varies from more than 1 cm to about 0.2 cm. The plants of many populations are glabrous, but throughout the range it is common to find plants that are short and sparsely pilose on leaves and stems.

4. **Flaveria brownii** A. M. Powell, sp. nov. TYPE: United States, Texas, San Patricio Co., roadsides and saline marshes, Port Aransas, Mustang Island, 30 Dec. 1974, *A. M. Powell 2802* (TEX, holotype; US, K, FSU, SRSU, GH, NY, F, KSC, isotypes)—FIG. 4.

Herbae perennes vel annuae longaevae 15–70 cm altae erectae decumbentesve. Folia sessilia 5–12 cm longa 0.2–0.7 cm lata glabra linearia. Capitula radiata aut discoidea 5–7-flora; phyllaria 5–6; ligulae ca. 2 mm longae. Achaenia 1.5–2 mm longa. Chromosomatum numerus $n = 18$.

Plants herbaceous perennials or long-lived annuals, 15–70 cm high, the stems many from the base, erect or decumbent, often purplish at maturity; leaves sessile, barely connate, 5–12 cm long, 0.2–0.7 cm wide, glabrous or essentially so, linear, tending to persist and wither in spirals at senescence, the margins entire or weakly serrate; capitulescence of numerous heads rather tightly aggregated in flat-topped, rather open corymbose panicles; heads radiate and discoid; involucres 4–5 mm long, oblong-angular, the phyllaries 5–6, boat shaped, acute, the one enclosing a ray floret conspicuously keeled; calyculate bracts linear; ray

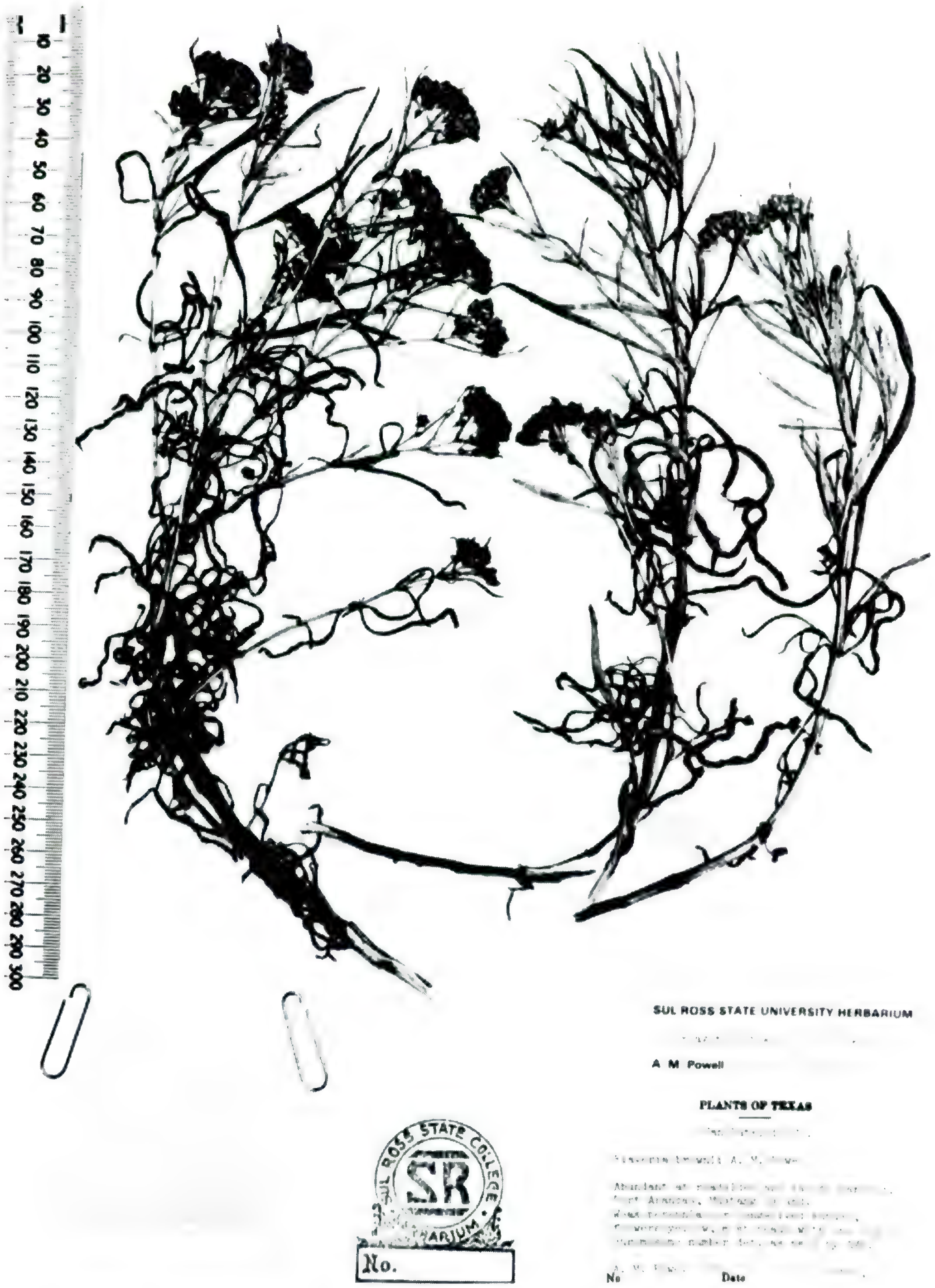

Figure 4. Phototype of *Flaveria brownii* A. M. Powell.

florets with the ligules ca. 2 mm long, oblong-elliptic; disc florets 5–10, the corollas 2.5–3 mm long, the tubes 0.8–1.2 mm long, the throats 1.2–1.5 mm long, the upper half expanded and funnelform, the lobes 0.5–1, acute; anthers 1.5 mm long; achenes linear, 1.5–2 mm long, the ray achenes longer; pappus absent; chromosome number, $n = 18$.

Saline, sandy, and marshy areas of the coastal flats and islands of the lower Texas Gulf Coast (Fig. 2).

REPRESENTATIVE SPECIMENS: UNITED STATES. TEXAS: Aransas Co., Aransas Refuge, *Cory 45791* (TEX). Rockport, *Tharp 4620* (TEX, US). Brooks Co., 21.7 mi SE of Hebbronville, *Cory 16950* (GH). Calhoun Co., below Seadrift, *Tharp s.n.* (TEX). Port O'Connor, *Tharp & Brown 48-179* (TEX). Kenedy Co., King Ranch, *Johnston 53·280·36* (TEX). 4.4 mi S of Armstrong, *Johnston 542265* (TEX). 6.7 mi N of Noria, *Stuessy & Roberts 3624* (OS). Kleberg Co., Riviera, *Reed 981* (US). Nueces Co., Mustang Island, *Gillespie 307* (TEX). Corpus Christi, *Tharp s.n.* (TEX). Padre Island, *Urbatsch 1547* (TEX). San Patricio Co., Aransas Pass, *Cory 51238* (MICH, NY). Willacy Co., Raymondville, *Shiller 786* (US).

This newly described species has long been confused in herbaria with *F. oppositifolia* to which it is superficially similar, but from which it is readily distinguished by its radiate heads among the discoid ones in each capitulescence. *Flaveria brownii* is probably most closely related to *F. floridana* of the Florida west coast as judged by their similar morphologies and ability to form seemingly fertile artificial F_1 and F_2 hybrids (Table 1). Synthetic hybrids also are readily formed with *F. oppositifolia*. *Flaveria brownii* also resembles *F. linearis*, especially those populations in Yucatán, Quintana Roo, and Cuba where the lower leaves of the plants tend to wither in spirals at senescence. Among the four species mentioned above, all somewhat related in the 5-phyllary line, *F. brownii* is the only one which has evolved C_4 photosynthesis (Fig. 1).

The occurrence of C_4 metabolism in *F. brownii* raises the question as to whether the phenomenon arose independently in the 5-phyllary line, as appears to be the case, or whether this species is actually derived from the original C_4 line which includes the annual species (Fig. 1). There is little morphological suggestion that *F. brownii* could have evolved from *F. vaginata* or the C_4 annuals. Morphologically *F. brownii* is closely tied to members of the 5-phyllary line, strongly suggesting that its C_4 capabilities were evolved at least as a second such event in the genus.

The specific epithet honors the late Walter V. Brown, an unusually perceptive investigator of the Kranz syndrome in Gramineae and other taxa, including *Flaveria*. In *Flaveria* he was particularly excited about the existence, in certain taxa, of Kranz morphology intermediates which suggest the active evolution of C_4 metabolism in the genus.

5. **Flaveria floridana** J. R. Johnston, Proc. Amer. Acad. Arts 39: 291. 1903. TYPE: United States, Florida, Lee Co., Sanibel Island, 29 Jan. 1896, *H. J. Webber 175* (US, holotype, not seen; F, MO, isotypes). Florida, Hog Island, 24 Nov. 1901, *S. M. Tracy 7341* (F, GH, MO, NY, US, WIS, syntypes). Florida, Manatee, *J. H. Simpson s.n.* (NY, US [2], syntypes).

F. linearis Lag. var. *latifolia* J. R. Johnston, Proc. Amer. Acad. Arts 39: 289. 1903, pro parte. TYPE: United States, Florida, Palm Beach Co., shore of Lake Worth, near Palm Beach, 31 Aug. 1895, *A. H. Curtiss 5524* (GH, holotype; GA, KSC, MO, NY, UC, US, isotypes).
F. latifolia (J. R. Johnston) Rydb., N. Amer. Fl. 34: 145. 1915, pro parte.
F. pinetorum Black, Bull. Torrey Bot. Club 50: 204. 1923 TYPE: United States, Florida, Lee Co., vicinity of Ft. Myers, 14 Dec. 1919, *P. C. Standley 18909* (US, holotype, not seen).
F. × *latifolia* (J. R. Johnston) Long & Rhamstine, Brittonia 20: 249. 1968, pro parte.

Plants herbaceous perennials, or perhaps annuals, 50–120 cm high, branching from the base, erect, essentially glabrous except sparsely pubescent on the upper peduncles; leaves opposite, connate or barely so, 5–14 cm long, 0.4–1.7 cm wide, linear, lanceolate, rarely subelliptic, the margins entire or minutely serrate or spinulose; capitulescence of corymbose panicles with numerous heads densely aggregated in subscorpioid clusters; heads radiate and discoid; involucres 3.6–4.5 mm long, suburceolate, oblong-angular, the phyllaries 5–6(–9), oblong or ovate-orbicular, obtuse or acute, an outer bract somewhat swollen and keeled basally, with 0–3 linear, hyaline, chafflike inner bracts; calyculate bracts linear, 0.3–1.5 cm long, often exceeding the length of the involucral bracts, and with modified upper peduncular leaves, visible above the top of the corymbs; ray florets with the ligules 2–2.8 mm long, 1.5–2 mm wide, obovate-spatulate, notched; disc florets 9–14, the corollas 2.7–3.2 mm long, the tubes 0.8–1 mm long, sparsely pubescent, the throats 1.3–1.5 mm long, funnelform, gradually tapering from the tube or more dilated distally, the lobes ca. 0.6 mm long, acute; anthers ca. 1.5 mm long; achenes of ray and disc florets of similar size, 1.2–1.8 mm long, oblong-oblanceolate or linear; pappus absent; chromosome number, $n = 18$.

This species is "restricted to saline, white sand near the beaches of brackish marshes" (Long & Rhamstine, 1968), lower Gulf Coast of Florida, especially common in the Tampa Bay area (Fig. 5).

REPRESENTATIVE SPECIMENS: UNITED STATES. FLORIDA: Charlotte Co., Punta Gordo, *Cornman 2091* (ARIZ, MO, US). Lee Co., Sanibel Island, *Brumbach 6538* (US). Captiva Island, *Brumbach 8159* (US). Little Gasperilla Island, *Fleak & Kreisel 1814* (NY). 5 mi E of Ft. Myers, *Kral 7546* (USF). Pine Island, *Lakela 30607* (USF). Hillsborough Co., 6 mi SE of Tampa, *Blanton 6483* (DS, LL, TEX, UC). Bahia Beach, *Lakela 24832* (LL, TEX, USF). Manatee Co., Longboat Key, *Long & Lakela 24582* (USF). Terra Ceia Island, *Shuey s.n.* (USF). Casey Key, *Ward & Burch 3161* (USF). Monroe Co.? keys of S Florida, *Chapman 2387* (US). Sneed's Island, *Tracy 6356* (GH, NY, US).

Flaveria floridana is distinguished from the other perennial species of Florida, *F. linearis*, by its long calyculate bracts that extend beyond the involucres and are visible above the corymbs (on herbarium sheets), larger heads with 10–15 florets, and funnelform disc corollas. Long & Rhamstine (1968) suggested that *F. floridana* was related to *F. oppostifolia*, but I believe that the species is closest to *F. brownii* of the lower Texas Gulf Coast. The two taxa are similar in their annual or weak perennial habits and both occupy similar habitats in limited coastal and coastal island areas. Among other traits the taxa are distinguished by leaves (and stems) in *F. floridana* which are darker green and thicker in texture. Presumably the Kranz anatomy of *F. brownii* results in a lighter coloration of the leaves.

6. **Flaveria linearis** Lag., Gen. & Sp. Nov. 33. 1886. TYPE: Cuba, Havana (not seen).

F. maritima H. B. K., Nov. Gen. Sp. Pl. 4: 285. 1820. TYPE: Cuba (not seen).
Selloa nudata Nutt., Amer. J. Sci. 5: 300. 1822.
Flaveria tenuifolia Nutt., J. Acad. Nat. Sci. Philadelphia 7: 81. 1834. TYPE: United States, East Florida, *Mr. Peale* (not seen).
Gymnosperma nudatum DC., Prodr. 5: 312. 1836.
Flaveria × *latifolia* (J. R. Johnston) Long & Rhamstine, Brittonia 20: 249. 1968, pro parte.

Plants herbaceous perennials, 30–80 cm high, the stems often purplish, erect, branching from the base, glabrous or pubescent mostly on the upper peduncles; leaves opposite, connate or barely so, 5–10(–13) cm long, 0.1–0.4(–1.5) cm wide, linear, the margins entire or serrulate-spinulose; capitulescence of flat-topped, corymbose panicles with numerous heads aggregated in clusters; heads radiate and discoid; involucres 3.3–4.5 mm long, oblong-angular, the phyllaries 5(–6), linear or oblong, obtuse-acute, the outer 2–3-keeled; calyculate bracts linear, 1–2.5 mm long; ray florets with the ligules 2–3 mm wide, oval or obovate-spatulate, 1–3-toothed; disc florets (2–)5–7(–8), the corollas 2.5–3.3 mm long, the tubes 0.8–1.2 mm long, glabrous or sparsely pubescent, the throats 1–1.5 mm long, tubular at the base, dilated to funnelform-campanulate above, the lobes ca. 0.5 mm long, acute; anthers 1.3–1.5 mm long; achenes of ray and disc florets of similar size, 1.2–1.8 mm long, linear; pappus absent; chromosome number, $n = 18$.

Near the coast and on offshore islands, Yucatán Peninsula, Mexico, widespread in the West Indies, and the most common *Flaveria* in Florida, "found in a wide variety of habitats" near the peninsular coast, including "in old fields, in roadside areas, margins of hammocks, in wet-cypress-pineland associations, in littoral communities, along canals, in mangrove swamps, etc." (Long & Rhamstine, 1968) (Fig. 5). In southern Florida the species frequently occurs in low, flat, rocky pineland in association with *Samolus*, *Bigelowia*, and *Borrichia*. Flowering throughout the year.

REPRESENTATIVE SPECIMENS: UNITED STATES. FLORIDA: Brevard Co., Melbourne Beach, *Lakela 28676* (GH). Broward Co., 10 mi W of Deerfield, *McCart 11262* (USF). Citrus Co., Shell Island, *Long 1308* (USF). Collier Co., Marco Island, *Lakela 27511* (USF). Dade Co., Coral Gables, *Demaree 10202* (DS, MO, US). Hendry Co., 4 mi W of LaBelle, *Henderson 63-1609* (TEX). Hernando Co., Bayport, *Cooley 5456* (USF). Hillsborough Co., *Blanton 6868* (CAS). Indian River Co., 5 mi N of Vero Beach, *Webb et al. 3612* (USF). Lee Co., Sanibel Island, *Cooley 904* (USF). Martin Co., near Indian Town, *Burch 20* (F, GH, MO, NY, TEX, UC, US). Monroe Co., Big Pine Key, *Almeda & Lakela 1934* (USF). Orange Co., Orlando, *Rhoades 6714* (F, UC). Osceola Co., Kissimmee Prairie, *McFarlin 3779* (MICH). Palm Beach Co., Lake Worth, *O'Neill 839* (MO, US). Pasco Co., Aripeka, *O'Neill 1045* (US). Pinnellas Co., Clearwater Beach, *McFarlin 3696* (MICH). Polk Co., Anastasia Key, *Jennings s.n.* (USF). St. Lucie Co., near Ft. Pierce, *Lakela 25238* (GH, USF). Volusia Co., Daytona Beach, *Ray 11131* (GH, USF). Wakulla Co., St. Marks Refuge, *Norris 663* (TEX).

BAHAMA ISLANDS. Andros Island, Kemp Bay, *Brace 5027* (F, NY). New Providence, *Britton 3150* (F, GH, NY).

CUBA. MATANZAS: *Alain 3049* (NY). PINAR DEL RÍO. *Britton & Cowell 9979* (NY).

MEXICO. QUINTANA ROO: Cozumel Island, *Steere 2985* (MICH). YUCATÁN: Progreso, *Gaumer 1147* (A, CAS, F, GH, MICH, MO, US). Perez Island, *Millspaugh 1753* (F, NY).

Long & Rhamstine (1968) noted that the Florida populations of *F. linearis*

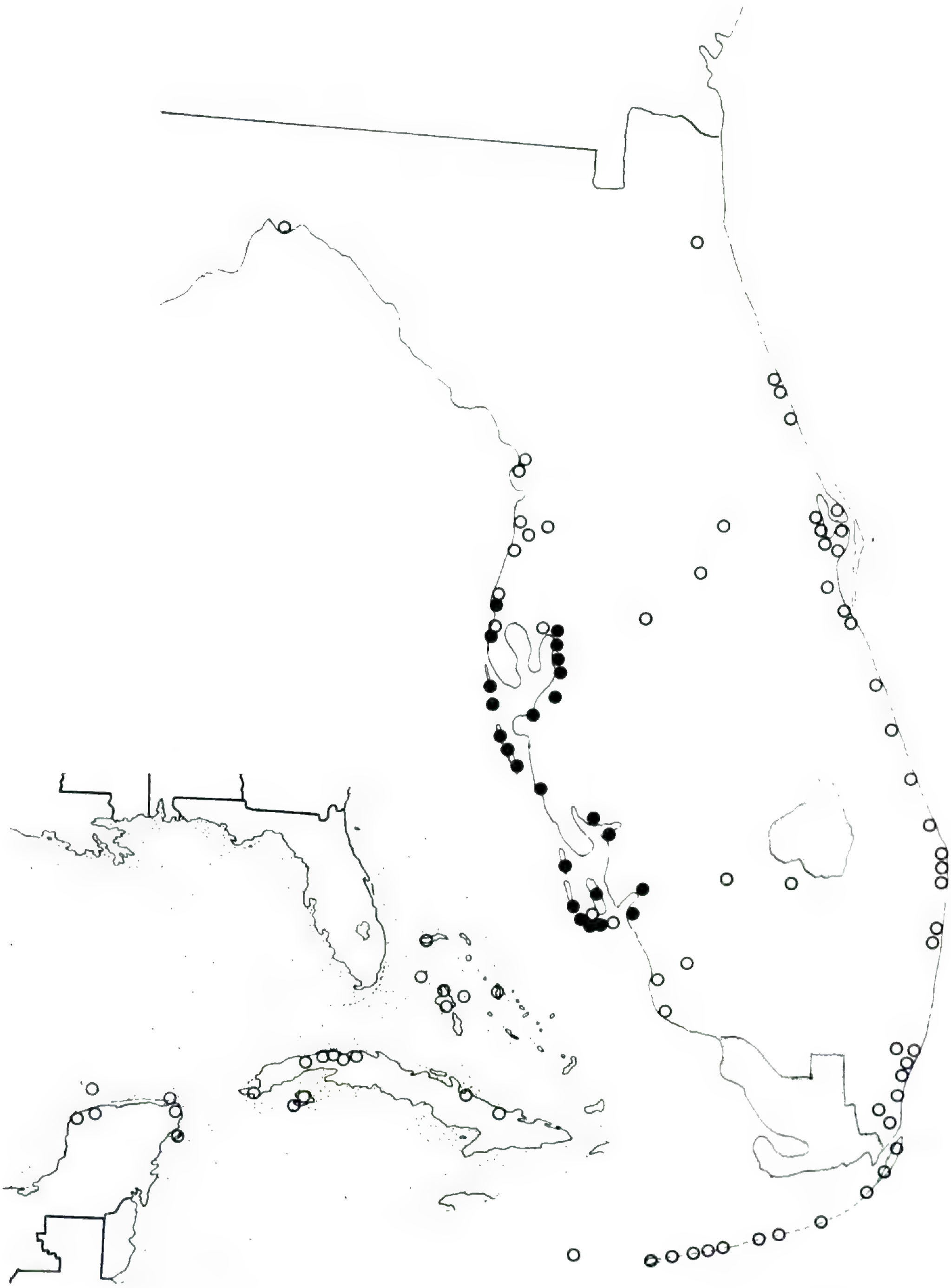

FIGURE 5. Distribution of *Flaveria floridana* (closed circles); *F. linearis* in Florida (open circles) and distribution in Yucatán, Quintana Roo, Cuba, and Bahama Islands (insert).

are more variable, particularly in leaf shape and size, than are those from the Bahamas, and they suggested that this variation originated through introgression from *F. floridana*. I also have found that the populations of *F. linearis* outside Florida in Quintana Roo, Yucatán, Cuba, and the Bahamas, are more homogeneous, and usually with narrower leaves. As in Florida, however, occasional plants from the West Indies and Mexico have broad leaves much like those which are theorized by Long and Rhamstine to have come from introgression in Florida.

My observations have shown that the populations of *F. linearis* from Yucatán and Cuba have a slightly different aspect than plants from Florida or the Bahamas. In general the Yucatán-Cuba plants appear slightly more robust, perhaps larger-stemmed, with shorter internodes, and with early senescent, twisting lower leaves, so that healthy leaves are on the middle and upper stems. The latter leaf trait also is characteristic of *F. brownii*. Plants of *F. linearis* from the Yucatán Peninsula have slightly larger heads, approaching those of *F. brownii*. The latter morphological features and distributional considerations (Fig. 5) suggest that *F. linearis* might have originated in Mexico, the distributional center of *Flaveria*, and then spread eastward through the West Indies and eventually into Florida. *Flaveria brownii* could have evolved as a C_4 adapted species and Texas Gulf Coast offshoot from the Yucatán population of *F. linearis*. Distributional and morphological considerations then might suggest that *F. floridana* evolved in the Tampa Bay area as an offshoot of *F. brownii*. It does not follow, however, that the C_3 taxon, *F. floridana*, would have originated from the C_4 *F. brownii* in that the latter condition is usually thought of as derived (Brown, 1977). Another possibility regarding the origin of *F. floridana* is that it became established as an offshoot of Mexican *F. linearis* at the same time as *F. brownii*. *Flaveria floridana* and *F. linearis* are ecologically isolated in Florida, and they could have co-existed there or not, in evolutionary history.

The source of variability in Florida populations of *F. linearis* is not fully understood. It is highly possible that hybridization with *F. floridana* and subsequent introgression is responsible for the variation, as Long & Rhamstine (1968) believed. Experimentally the two species are interfertile (Table 1), but further study of the situation in the field remains to be accomplished.

In addition to hybridization and introgression between *F. linearis* and *F. floridana*, Long & Rhamstine (1968) proposed the existence of a stable species, *F.* × *latifolia*, of the same hybrid origin. The hybrid species is supposedly intermediate morphologically, except sometimes with wider leaves, and was said by Long and Rhamstine to occur in a type of hybrid habitat, i.e., fill material dredged from the ocean and used in land development, and also "in dune and strand vegetation along the lower Gulf Coast." Artificial *F. linearis* × *F. floridana* hybrids (Table 1) conform morphologically with specimens annotated by Long and Rhamstine as *F.* × *latifolia*. Thus experimental evidence supports the possibility that natural hybridization has occurred between *F. linearis* and *F. floridana*.

At this time, however, I am not able to recognize the hybrid species *F.* × *latifolia*. My observations suggest that hybridizations between *F. linearis* and

F. floridana have occurred, but that the events were uncommon and sporadic, and that there exists no stable population worthy of specific status. Furthermore, my studies show that *F. floridana* is restricted to the lower Gulf Coast of Florida (Fig. 5) while *F. linearis* is essentially allopatric and widespread over much of the peninsula, although the distributions do overlap in Hillsborough, Pinellas, and Lee counties (Fig. 5). Long & Rhamstine (1968) show one locality of *F. floridana* in Palm Beach County on the East Coast, and they show *F. linearis* to be regionally sympatric with *F. floridana* in the vicinity of Tampa Bay and south along the Gulf Coast. Richard P. Wunderlin (pers. comm.) is of the opinion that *F. linearis* and *F. floridana* are sympatric somewhere in south Florida and that hybridization probably occurs between them. Further studies will be necessary to resolve the exact distributions of the two species, to clarify the extent of their ecological isolation, and to evaluate the extent to which hybridization might have contributed to the variability of *F. linearis* in Florida. If hybrids exist, then one would expect to find them in areas of sympatry and not scattered over the peninsula as indicated by Long & Rhamstine (1968), unless the "hybrids" are progeny of a stabilized species of hybrid origin as proposed by the latter authors.

Distinguishing characters of *F. linearis* include: usually narrow, linear leaves; rather short, linear calyculate bracts; oblong-angular involucres; heads rather small, with 5–8(–9) florets; throats of disc corollas tubular at base and abruptly expanded distally to funnelform-campanulate. Long & Rhamstine (1968) report that an extensive population of *F. linearis* was found growing with *F. bidentis* on Malabar Cape, Brevard County, but with no indication of hybridization.

7. **Flaveria sonorensis** A. M. Powell, sp. nov. TYPE: Mexico, Sonora, Agua Caliente, N of Alamos, 2 Nov. 1939, *H. S. Gentry 4852* (UC, holotype; DS, MICH, NY, isotypes).

Herbae perennes ad 1 m altae. Folia 6–14 cm longa 0.3–1.5 cm lata glabra linearia vel lanceolata margine spinuloso-serrata. Capitula radiata aut discoidea, 5–7-flora; phyllaria 4–5. Achaenia 1.2–1.5 mm long. Chromosomatum numerus $n = 18$.

Plants herbaceous perennials, to 1 m high; leaves barely connate, 6–14 cm long, 0.3–1.5 cm wide, glabrous, linear or lanceolate, the margins serrate or spinulose-serrate; capitulescences of flat-topped panicles with numerous heads in each cluster; heads radiate and discoid; phyllaries (4–)5, linear; disc florets 5–7, the corollas 2.5–3 mm long; achenes 1.2–1.5 mm long, the ray achenes slightly longer than some disc achenes, equal to others; pappus absent; chromosome number, $n = 18$.

Watershed of the Río Mayo, southern Sonora, short-tree forests of tropical Sonora, often close to warm mineral springs, 160–1,000 m, and near Batopilas in adjacent Chihuahua (Fig. 2).

REPRESENTATIVE SPECIMENS: MEXICO. CHIHUAHUA: near Batopilas, *Goldman 240* (GH, NY, US). SONORA: San Bernardo and vicinity, *Arguelles 82* (LL, TEX, US). Salitral, Río Mayo, *Gentry 1274* (F, GH, MICH, NY, TEX, UC). Aguas Calientes, *Kuntze 23481* (NY, UC). Rancho Salitral near San Bernardo, *Martin 5* (ARIZ).

This previously undescribed entity was discovered among borrowed specimens of *F. robusta*, which *F. sonorensis* resembles in capitulescence and floral aspects. *Flaveria sonorensis* is delimited by its rather narrow spinulose-serrate or serrate leaves, (4–)5 linear phyllaries, 5–7 florets per head, and distribution. The relationship of *F. sonorensis* is not clear, but its heads with five phyllaries suggest that it may not belong with *F. robusta* and the 3-phyllary line, even though these species are of similar habit and distribution (Fig. 3). Instead, *F. sonorensis* may be related to *F. linearis*, a radiate species of the 5-phyllary line with a propensity for coastal and inland distribution.

8. **Flaveria angustifolia** (Cav.) Pers., Syn. Pl. 2: 489. 1807.

Milleria angustifolia Cav., Icon. Pl. 3: 12. 1794. TYPE: Mexico, "Nova Hispania," (K, lectotype).
Flaveria integrifolia Moç. & Ses. in DC., Prodr. 5: 635. 1836, pro syn.
F. radicans Moç. & Ses. in DC., Prodr. 5: 635. 1836, pro syn.
F. elata Klatt, Leopoldina 23: 146. 1887. TYPE: Mexico, Tehuacán, *Leibman 267* (not seen).

Plants herbaceous perennials, 0.5–1 m high, erect and spreading; leaves opposite, connate, the upper ones 8–12 cm long, 1–2.2 cm wide, glabrous, linear-lanceolate, the margins serrulate-spinose to minutely so, rarely entire; capitulescence of corymbose panicles with numerous heads aggregated in dense scorpioid clusters; heads radiate and discoid with a ray floret in most heads; involucres 4.3–5 mm long, oblong-angular, the phyllaries 3–4, boat shaped, oblong and acute, usually with an outer phyllary enclosing the ray floret, the phyllary shorter, broader, usually with a prominent, curved, swollen corky keel at maturity, the 2 other main phyllaries, if mature, may be corky keeled on the lower half, an inner 4th phyllary smaller, linear; calyculate bracts 2–3 mm long, sublinear or subovate, somewhat cupped- and sickle-shaped; ray florets with the ligules (1.5–)2–3 mm long, linear-oblong, 2–3-toothed; disc florets 5–7, the corollas 3–3.5 mm long, the tubes 1–1.3 mm long, moderately villous, the throats 1.5–1.7 mm long, the lower half tubular, the upper half expanded into a campanulate shape, the lobes ca. 0.5 mm long, acute; anthers ca. 1.5 mm long; achenes of the ray and disc florets the same size, (1–)1.5–2(–2.5) mm long, linear or narrowly oblanceolate, rarely nearly obovate; pappus absent; chromosome number, unknown.

Sandy or loamy soils in open fields and in sclerophyllous scrub, Puebla and Oaxaca, to Mexico (Distrito Federal) and Guerrero (Fig. 3).

REPRESENTATIVE SPECIMENS: MEXICO. DISTRITO FEDERAL: Chapultepec, *Schaffer 16* (GH). GUERRERO: Coyuca-Tinajas, *Hinton 5844* (K, MO, US). OAXACA: Ca. 1 mi N of Tamazulapan, *King 2930* (DS, MICH, NY, TEX, UC, US). Cerro Solo, 7 km NE of Tepelmeme de Morelos, *Cisneros 2419* (MICH). PUEBLA: Puebla, *King 2623* (DS, MICH, NY, TEX, UC, US). Fields near Puebla, *Pringle 4749* (GH, MICH, MO, NY, UC, US). Near Tehuacán, *Rose & Hay 5871* (US).

Flaveria angustifolia is closely related to *F. pringlei* and the taxa have often been confused by superficial examination of herbarium specimens, but *F. angustifolia* can be delimited easily by its radiate heads. The species is also distinguished usually by its mostly sessile, linear-lanceolate leaves with serrulate-spinulose margins, distally expanded throats of the disc corollas, and corky-keeled

phyllaries. Leaf measurements and observations in the descriptions of *F. angustifolia* and related shrubby species were taken from the upper portions of the plants that were preserved as specimens.

9. **Flaveria pringlei** Gandoger, Bull. Soc. Bot. Fr. 65: 42. 1918. TYPE: Mexico, Puebla, fields at Tehuacán, 20 Dec. 1895, *C. G. Pringle 7369* (P? holotype; US, isotype).

Plants perennial herbs, shrubs with many erect stems from the base, or small trees, 1–4 m high; leaves opposite, the lower leaves petioled (0.5–1 cm) and barely connate, the upper leaves sessile and connate or short petioled, 7–13 cm long, 1.5–4.5 cm wide, glabrous, lanceolate-elliptic to broadly so or ovate, the margins entire; capitulescence of corymbose panicles with numerous heads densely aggregated in clusters; heads discoid, or rarely with a seemingly abortive ray floret enclosed by the outer phyllary, the ligule erect and not extending from the bract; involucres 4–5 mm long, tubulo-angular, the phyllaries 3–4, with 2 outer and 2 inner ones, the outer phyllaries boat shaped; calyculate bracts 1.5–3 mm long, subdeltoid, linear, rarely boat shaped; disc florets 7–9, the corollas 3–4 mm long, the tubes 1.5 mm long, sparsely villous or naked, the throats 1–1.5 mm long, funnelform, the lobes ca. 1 mm long, acute; anthers 1.5–2 mm long; achenes (1.2–)1.5–2 mm long, linear or narrowly oblanceolate; pappus absent; chromosome number, $n = 18, 36$.

Rather arid and at least sometimes gypseous habitats, scattered localities, waste places, cultivated fields, roadsides, deciduous woods, in and near the Tehuacán Valley, Puebla and Oaxaca, west to Guerrero (Fig. 3).

REPREENTATIVE SPECIMENS: MEXICO. GUERRERO: 7 mi N of Chilpancingo, *King 4174* (F, MICH, NY, UC, US). Ca. 35 km NNW of Chilpancingo, *McVaugh 22198* (DS, LL, MICH, NY, TEX). OAXACA: 6 mi NW of Huajuapan de León, *Dillon 681* (LL, TEX). Ca. 7 mi N of Huajuapan de León, *King 2532* (DS, MICH, TEX). 54 mi SE of Puebla-Oaxaca border, *King 6439* (MO, US). 30 mi NNW of Huajuapan de León, *Turner P-50* (TEX). PUEBLA: 18–20 km NW of the Oaxaca-Puebla border, *Anderson & Anderson 5647* (MICH). 5 mi SW of Tehuacán, *Breedlove 14188* (CAS, MICH, NY). 1 mi SE of Tehuacán, *Cronquist & Sousa 10388* (NY). 16 mi S of Esperanza, *Hartman et al. 3834* (LL). 3 mi N of the Oaxaca-Puebla border, *King 2534* (DS, MICH, TEX). S of Petlalcingo, *Langman 4152* (US). 5 km NW of Petlalcingo, *Rzedowski 28942* (MICH, TEX). 1 mi S of Rija, 16 mi S of the Morelos border, *Walker 72009* (NY).

On herbarium sheets *F. pringlei* is readily distinguished from the closely related and morphologically similar *F. angustifolia* by its discoid heads. The former species also differs by its usually broader, ovate leaves with entire margins, disc corollas with funnelform throats, and somewhat thickly keeled outer phyllaries.

Abortive ray florets were seen in two collections of *F. pringlei*, the type collection and *King 2533* (Puebla, near Petlalcingo). In certain heads the florets with very small, erect ligules were found enclosed by an outer (shortest) phyllary, not at all evident except by dissection. I believe that *F. pringlei* evolved from the radiate *F. angustifolia*. The only instances of polyploidy ($n = 36$) known in *Flaveria* were found in two collections of *P. pringlei* (*Dillon 681*; *Hartman et al. 3834*). The known distributions of *F. pringlei*, *F. angustifolia*, and *F. vaginata* are

somewhat overlapping (Fig. 3), and it is possible that hybridization has occurred among the taxa.

10. **Flaveria vaginata** B. L. Robinson & Greenman, Proc. Amer. Acad. Arts 32: 48. 1896. TYPE: Mexico, Oaxaca, between Coixtlahuaca and Tamuzulapan, 2,300–2,600 m, 12 Nov. 1894, *E. W. Nelson 1933* (GH, lectotype; K, isolectotype).

Plants shrubby perennials, ca. 1 m high, the stems several, erect, with short grayish woolly pubescence especially on the peduncles; leaves opposite, sessile, connate, often fascicled in the axils, 3–8 cm long, 0.2–0.6 cm wide, pale green, rather densely short pubescent, linear-subulate, the margins entire, ciliated; synflorescence of corymbose-paniculate, hemispherical glomerules, with numerous heads tightly aggregated in simulation of normal composite heads, the ligulate heads mostly peripheral; heads radiate and discoid; involucres 3.5–4 mm long, oblong-angular, the phyllaries 3(–4), boat shaped, hyaline; calyculate bracts 1.5–3 mm long, ovate-orbicular or sickle shaped; ray florets with the ligules 2–4 mm long, oblong-elliptic, 2–3-toothed; disc florets 5–8, the corollas 3.2–3.5 mm long, the tubes ca. 1 mm long, moderately pubescent or naked, the throats ca. 1 mm long, the upper half expanded to a subcampanulate shape, the lobes ca. 0.5 mm long, acute; anthers ca. 1.5 mm long; ray achenes ca. 2 mm long, the disc achenes ca. 1.5 mm long, both linear or narrowly oblanceolate; pappus absent; chromosome number, unknown.

Known only from the type collection and the one other specimen cited (Fig. 3).

REPRESENTATIVE SPECIMEN: MEXICO. PUEBLA: 7 mi W of Izúcar de Matamoros, *King 2922* (DS, MICH, NY, TEX, UC, US).

The type specimens of *F. vaginata* are distinctive in the densely pubescent upper herbage, sessile linear-subulate leaves, and heads aggregated into hemispherical glomerules with peripheral radiate heads. The *King 2922* collection shows minor differences in the disc corollas but otherwise compares favorably with the types. The species is closely related to *F. angustifolia* and *F. pringlei* of the same general distribution.

The shrubby habit, rather thick leaves, and radiate heads of *F. vaginata* and *F. angustifolia* suggest primitiveness in the 3–4-phyllary line of Puebla-Oaxaca species (Fig. 1), but the glomerulate heads (synflorescence) and C_4 metabolism of *F. vaginata* suggest a more derived lineage. In fact, it is from *F. vaginata* that the C_4 annual species (Fig. 1), all with radiate synflorescences, may be derived.

11. **Flaveria cronquistii** A. M. Powell, sp. nov. TYPE: Mexico, Puebla, 6 mi NW of Teotitlán and 33 mi SE of Tehuacán, 1,100 m, 22 Oct. 1965, *A. cronquist & M. Sousa 10385* (NY, holotype; CAS, F, GH, KSC, MICH, TEX, US, WIS, isotypes).

Frutex 1–1.7 m altus. Folia 7–10 cm longa 0.3–1.5 cm lata, succulenta glabra linearis vel lanceolata petiolis 0.6–1.3 cm longis. Capitula eradiata 7-flora; phyllaria 3. Achaenia 1.5–1.8 mm longa. Chromosomatum numerus $n = 18$.

Plants shrubs and small trees, 1–1.7 m high; leaves opposite, barely connate, 7–10 cm long, 0.3–1.5 cm wide, slightly succulent, glabrous, linear or lanceolate, the margins entire, the petioles 0.6–1.3 mm long; capitulescence of rather open, corymbose, flat-topped panicles, with numerous heads rather loosely aggregated in each cluster; heads discoid; involucres ca. 4 mm long, subcylindrical-angular, the phyllaries 3, boat shaped, obtuse; calyculate bracts linear, ca. 1 mm long; disc florets 7, the corollas 3–3.5 mm long, the tubes 1–1.2 mm long, the throats 1.2–1.5 mm long, tubular or slightly funnelform, the lobes 0.5–1 mm long, reflexed, linear; anthers ca. 1.5 mm long; achenes 1.5–1.8 mm long, nearly linear or narrowly oblanceolate; pappus absent; chromosome number, $n = 18$.

Rocky limestone (possibly gypseous) areas of the Tehuacán Valley, usually in thorn-scrub vegetation, Puebla-Oaxaca, Mexico (Fig. 3).

REPRESENTATIVE SPECIMENS: MEXICO. OAXACA: 8 km SE of Teotitlán, *Cronquist 11240* (MO, US). PUEBLA: 8 mi SE of Coxcatlán, *Anderson & Anderson 5341* (MICH). 5 mi SW of Tehuacán, *Breedlove 14189* (CAS, MICH, NY). Amatitlán, *Miranda 2516* (GH). Tehuacán, *Purpus 5626* (F, NY, UC, US).

Flaveria cronquistii is delimited from other species of the Tehuacán Valley region by its subcylindrical discoid heads arranged in rather loose, flat-topped corymbs, linear (or lanceolate) leaves, pubescent and indistinct tips of the style branches, and barely funnelform throats of the disc corollas. The taxon perhaps most closely resembles *F. robusta* of Colima-Michoacán, but its shrubby habit, semisucculent leaves, small heads, and distribution also suggest a relationship with *F. angustifolia* and allies. Both *F. cronquistii* and *F. vaginata* exhibit C_4 metabolism (Fig. 1) suggesting an ancestral connection on this basis, although the radiate glomerulelike inflorescence of *F. vaginata* is not at all like that of *F. cronquistii*.

The *Miranda 2516* collection from Puebla is here assigned to *F. cronquistii* although it is anomalous in the following characters: leaves broadly lanceolate, longer (to 13 cm) and wider (to 3.2 cm); calyculate bracts ovate and obtuse; florets 3; disc corollas slightly shorter with tubular throats; style branches glabrous with sharply defined tips; achenes smaller, 1.2–1.3 mm long.

The specific epithet of this newly described species is intended to honor Dr. Arthur Cronquist of the New York Botanical Garden who has collected the species and other Flaverias, and who is widely recognized for his contributions to the systematics of Asteraceae.

12. **Flaveria robusta** Rose, Contr. U.S. Natl. Herb. 1: 337. 1895. TYPE: Mexico, Colima, 27–28 Feb. 1891, *E. Palmer 1299* (GH, lectotype; K, MO, NY, UC, isolectotypes).

Plants perennial herbs or shrubs, (60–)100–200 cm high, the stems essentially glabrous; leaves opposite, connate or nearly so, 5–14 cm long, 0.8–3.4 cm wide, somewhat fleshy, glabrous, lanceolate, lance-elliptic, linear-lanceolate, or linear, the margins serrate or minutely so, or entire, the petioles 1–2.5 mm long; capitulescence of rather open corymbose, flat-topped panicles with numerous heads in each cluster; heads radiate and discoid; involucres ca. 3 mm long,

oblong-angular or subcylindrical, the phyllaries usually 3, boat shaped or linear; calyculate bracts linear, ca. 1 mm long; ray florets with the ligules 2–2.5 mm long, oblong-obovate, notched apically; disc florets usually 3, the corollas 2.5–3 mm long, the tubes ca. 1 mm long, glabrous or sparsely glandular, the throats ca. 1.5 mm long, funnelform, the lobes ca. 0.8 mm long, reflexed, linear; anthers 1–1.7 mm long; achenes of the disc florets ca. 1.2 mm long, those of the ray florets ca. 1.5 mm long, subobovate or oblanceolate; pappus absent; chromosome number, $n = 18$.

Gypsum and slate, sandy clay, deciduous woodland, or open rocky slopes, often weedy at roadsides, or with cacti and bromeliads, 340–500 m, Colima and adjacent Michoacán (Fig. 3).

REPRESENTATIVE SPECIMENS: MEXICO. COLIMA: 20 mi S of Colima, *Alava & Cook 1693* (MICH, UC). Armeria, *Jones 276* (US). Ca. 11 mi SSW of Colima, *McVaugh & Koelz 1044* (LL, MICH, TEX). 10 mi SSW of Colima, *McVaugh 15529* (MICH, US). 5–10 mi N of Tecomán, *Thompson & Fields 321* (TEX). MICHOACÁN: Ca. 5 km SW of Coahuayana, *Feddema 2732* (CAS, MICH, TEX).

The large habit, small heads with three phyllaries and geographical considerations suggest that *F. robusta* is related to *F. angustifolia* and allies, and derived therefrom. The species is distinguished by its showy radiate heads arranged in rather open panicles, leaf shape and size, various floral characters, and distribution.

13. **Flaveria bidentis** (L.) Kuntze, Rev. Gen. 3: 148. 1898.

Ethulia bidentis L., Mant. 110. 1767. TYPE: "India"? (LINN, not seen).
Eupatorium chilense Molina, Sagg. Chile 142. 1789.
Milleria chiloensis Juss., Gen. Pl. 187. 1789, pro syn.
Flaveria chilensis Juss.; J. F. Gmel., Syst. Nat. 2: 1269. 1791.
Milleria contrayerba Cav., Icon. 1: 2. 1791.
Vermifuga corymbosa Ruiz & Pavón, Syst. Veg. Fl. Per. 216. 1798.
Flaveria contrayerba Pers., Syn. Pl. 2: 489. 1807.
F. capitata Juss.; Smith, in Rees, Cycl. 14: 1810. *Flaveria* no. 1.
F. bonariensis DC., Prodr. 5: 635. 1836.
F. bidentis var. *angustifolia* Kuntze, Rev. Gen. 3: 148. 1898. TYPE: South America, Argentina, Córdoba (not seen).

Plants delicate or robust annuals, (15–)25–100 cm high, the stems often purplish, sparsely-villous; leaves opposite, rather light green, 5–12(–18) cm long, 1–2.5(–7) cm wide, glabrous or densely short-pubescent, lanceolate-elliptic, serrate or spinulose-serrate, the petioles of the main leaves 0.3–1.5 cm long, the bases nearly connate, the blades of the upper leaves usually connate; capitulescence of tightly aggregated heads in scorpioid cymes, the heads alternate on short axes; heads obscurely radiate; involucres ca. 5 mm long, oblong and angular, the phyllaries 3(–4), concave and rounded or obtuse apically; calyculate bracts 1–2; ray corollas short, 1–2 mm long, pale yellow, the ligule not or barely protruding from the closed bracts, erect, ovate-oblique, acute, ca. 1 mm long or less; disc florets (2–)3–8, the corollas ca. 2.3 mm long, the tubes ca. 0.8 mm long, the throat ca. 0.8 mm long, funnelform, the lobes ca. 0.5 mm long, acute; anthers ca. 1 mm long; achenes of the disc florets ca. 2 mm long, those of the ray florets ca.

FIGURE 6. Distribution of *Flaveria bidentis* in South America.

2.5 mm long, larger, oblanceolate or subclavate; pappus absent; chromosome number, $n = 18$.

A weed in moist places on waste ground, near rivers, streams, and barrancas, in fields, pastures, disturbed ground, near streets and sidewalks in towns, clay-gravel, or sand, 250–2,800 m. South America (Fig. 6); ballast and waste ground

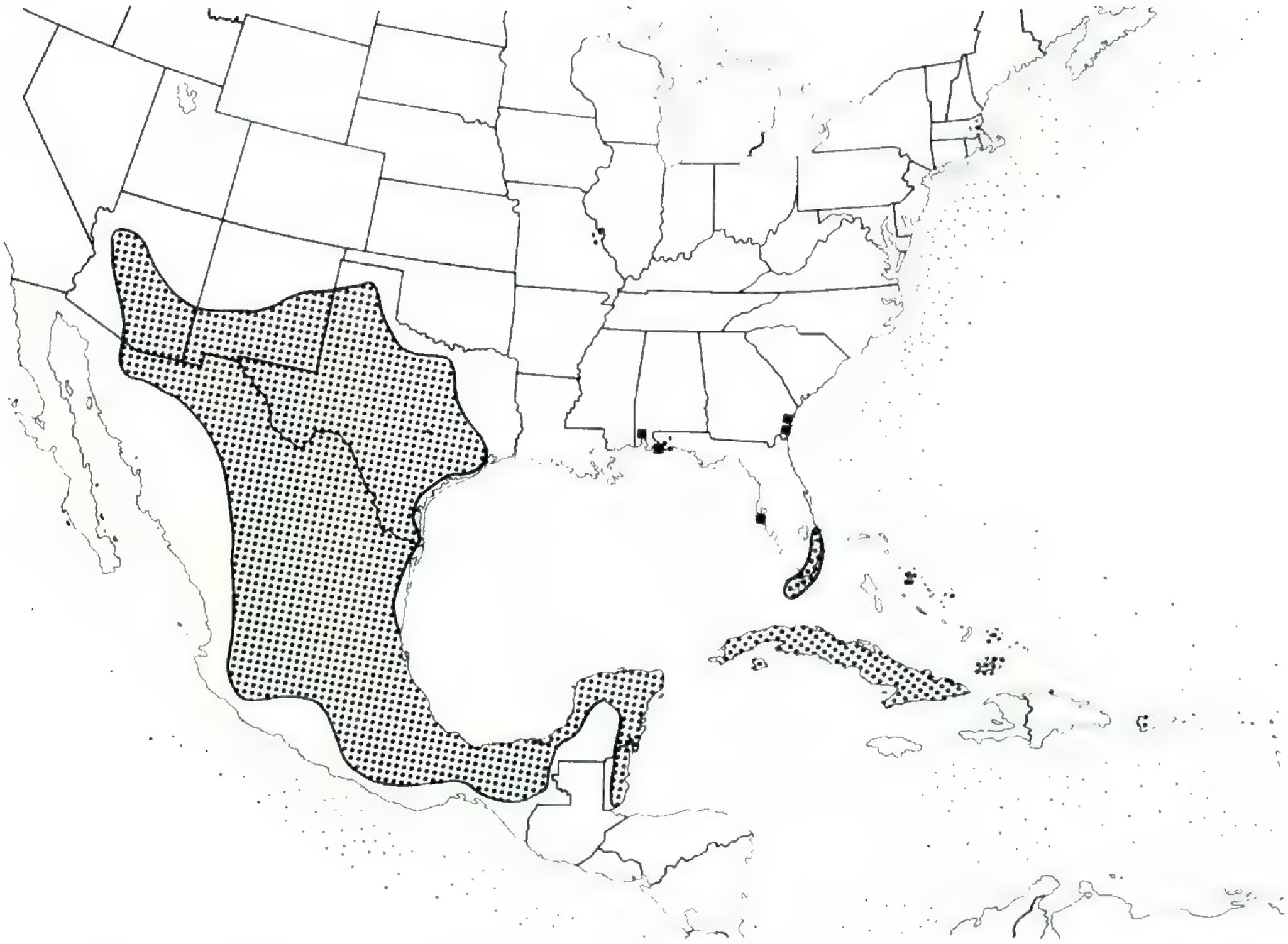

FIGURE 7. Generalized distribution of *Flaveria trinervia* in North America, Central America, and the West Indies (dots); Old World distribution of *F. trinervia* not plotted; distribution of *F. bidentis* in the United States (squares).

near wharfs and the shore, southeastern Gulf Coast, United States (Fig. 7); a weed in Great Britain, the West Indies, Egypt, and southern Africa.

REPRESENTATIVE SPECIMENS: ARGENTINA. BUENOS AIRES: Saladillo, *Cabrera 6426* (US). CATAMARCA: Belen, *Cabrera 1195* (LL, TEX). CHACO: Presidente de la Plaza, *Malvarez 862* (DS). CÓRDOBA: Córdoba, *Huidobro 461* (US). CORRIENTES: Saladas, *Schwarz 9573* (TEX). FORMOSA: Pilcomayo River, *Morel 8339* (US). JUJUY: Humahuaca, *Venturi 8773* (GH, US). LA PAMPA: Catriló, *Furtuna s.n.* (A). LA RIOJA: Famatina, *Paz s.n.* (A, F, UC). MENDOZA: Godoy Cruz, *Leal 8390* (A, UC). MISIONES: Apostoles, *Huidobro 4699* (TEX). NEUQUEN: General Roca, *Fischer 249* (F, GH, MO, NY, US). SALTA: Mira Flores, *Huidobro 551* (US). SAN JUAN: Jachál, *Cuezzo 1920* (F). SAN LUIS: San Martín, *Varela 521* (F). SANTIAGO DEL ESTERO: Río Salado, *Job 1102* (NY). TUCUMÁN: Tucumán, *Venturi 332* (A, US).

BOLIVIA. CHUQUISACA: La Loma, *Espinosa 494* (F). COCHABAMBA: Cochabamba, *Bang 968* (F, GH, MO, NY, US). LA PAZ: Río Palca Valley, *Julio 20* (US). SANTA CRUZ: Cabezas, *Peredo 396* (A). TARIJA: Tarija, *Fiebrig 2227* (GH).

BRAZIL. MATO GROSSO: Corumbá, *Robert 786* (K).

CHILE. ATACAMA: Copiapó, *Johnston 5000* (GH, US). SANTIAGO: Santiago, *Claude-Joseph 2233* (US). TARAPACÁ: Arica, *Jaffuel 1064* (GH). VALPARAÍSO: Quillota, *Bridges 491* (K).

ECUADOR. IMBABURA: Between Ibarra and Salinas, *Asplund 10449* (CAS, NY, US). LOJA: Loja, *Espinosa 494* (NY). MANABI: Zapallo, *Eggers 15704* (F, US).

PARAGUAY. BOQUERÓN: Gran Chaco, *Pride s.n.* (K). CONCEPCIÓN: Sierra de San Luis, *Kurtz 8551* (NY).

PERU. AMAZONAS: Valley of Río Utcubamba, *Wurdack 2065* (F, US). APURIMAC: Andahuaylas, *Herrera 1486* (GH). AREQUIPA: Arequipa, *Rose 18816* (US). CUZCO: *Bues s.n.* (F,

GH). HUÁNUCO: 5 km N of Huánuco, *Canne et al. 211* (ASU, OS, US). ICA: Ica, *Lauderman 4023* (K). LA LIBERTAD: Chicama Valley, *Smith 16* (US). LIMA: San Lorenzo Island, *Anderson s.n.* (US). Chosica, *Grant 7407* (GH). TACNA: Near Tacna, *Metcalf 30348* (GH, MO, US).

UNITED STATES. ALABAMA: Mobile Co., *Mohr s.n.* (US). FLORIDA: Escambia Co., Pensacola, *Curtiss 6495* (DS, GH, K, MO, NY, UC, US). Hillsborough Co., Mullet Key, *Long 1261* (DS). GEORGIA: McIntosh Co., Durien, *Biltmore? 6723* (US). Glynn Co., Brunswick, *Harper 1521* (F, GH, MO, NY, US).

GREAT BRITAIN. Gloucester, *Sandwith 5744* (K).

ANTIGUA. *Box 1022* (F, MO, UC, US).

CUBA. *Wright s.n.* (K).

DOMINICAN REPUBLIC. Barahona, *Liogier 18314* (NY, US).

PUERTO RICO. MAYAGUEZ: Guanica, *Liogier 10436* (NY).

BOTSWANA. 5 mi S of Palapye, *Leach & Noel 268* (K).

EGYPT. *Pfund 1586* (US).

ETHIOPIA. *Pappi 2193* (F).

RHODESIA. *Wild 2784* (K).

LESOTHO. *Clirhaiulan 717* (K).

SOUTH AFRICA. NATAL: Zululand, *Ward 2451* (K). TRANSVAAL: Pretoria, *Strey 3095* (A).

SOUTH WEST AFRICA. *Meyer 1115* (UC).

SWAZILAND. *Compton 40919* (K).

The weedy species *Flaveria bidentis* is widespread and well established in South America, and probably should be regarded as native to that country. In floral structure *F. bidentis* is perhaps least advanced of the annual species. The capitulescence is somewhat scorpioid, but contracted, as though it were derived from *F. angustifolia*. *Flaveria bidentis* also is characterized by pubescent stems, lanceolate-elliptic, bluish green leaves (thinner in texture than in *F. trinervia*), 3(–4) phyllaries, 2–8 florets per head, and reduced ray corollas.

Flaveria bidentis perhaps evolved as an annual C_4 prototype in Mexico from the perennial *F. vaginata* (C_4) line (Fig. 1), and reached South America as a self-compatible colonizer during the Pliocene or Pleistocene, a time much other bicontinental distribution was taking place (Raven, 1963). The species then must have flourished in South America, subsequently spreading as a weed to other parts of the world. Some specimens of *F. bidentis* from the West Indies and other areas are smaller, thinner plants with narrow leaves and more lax capitulescences, but these are seemingly ecological variances without taxonomic significance. The taxon is related to *F. campestris* and *F. trinervia*.

14. **Flaveria campestris** J. R. Johnston, Proc. Amer. Acad. Arts 39: 287. 1903. TYPE: United States, Missouri, near Courtney, 10 Sep. 1890, *B. F. Bush 51* (US, lectotype).

Flaveria angustifolia A. Gray, Mem. Amer. Acad. Arts, n.s., 4: 88. 1849. Hyponym., Coult., Contr. U.S. Natl. Herb. 2: 234. 1892, non *F. angustifolia* Pers. 1807.

Plants delicate or robust annuals, 18–70 cm high, the stems mostly erect, often purplish, glabrous except tufted-pubescent in the axils; leaves opposite, barely connate, 3–9 cm long, 0.6–2.2 cm wide, glabrous, lanceolate or linear-lanceolate, the margins serrate to weakly so, or spinulose-serrate; capitulescence of tightly aggregated heads in subglomerules; heads radiate or discoid, the radiate heads peripheral; involucres 6–7 mm long, urceolate or oblong, angular, the phyllaries 3, boat shaped, keeled, elliptic, obovate or oblong-obovate, acute;

calyculate bracts 2, 1–3 mm long, unequal, linear-lanceolate; ray florets with the ligules yellow, 1.5–2.5 mm long, ovate, notched; disc florets 5–6(–8), the corollas 2.5–3.5 mm long, the tubes 0.8–1.3 mm long, the throats 1.2–1.7 mm long, funnelform, the lobes 0.5–0.8 mm long, acute; anthers 1–1.5 mm long; achenes 2.8–3.6 mm long, those of the ray florets noticeably larger and longer by ca. 0.2 mm, oblanceolate, linear, or oblong; pappus absent; chromosome number, $n = 18$ (9).

Seemingly always in saline soils, at the margins of lakes, ponds, streams, in flood plains, or in disturbed pastures, 1,000–1,600 m, Missouri southwest to Kansas, Colorado, New Mexico, and to Arizona, and south of Oklahoma and north Texas (Fig. 2).

REPRESENTATIVE SPECIMENS: UNITED STATES. ARIZONA: Navajo Co., 5 mi SE of Winslow, *Crutchfield 912* (LL). COLORADO: Bent Co., Las Animas, *Osterhout 4138* (NY). Mesa Co., Grand Junction, *Cowen 2903* (MO, NY, US). Otero Co., E of Lajunta, *Drouet et al. 4073* (F). Prowers Co., 4 mi W of Lamar, *Lindstrom 1660* (KSC). Pueblo Co., Lake Minnequa near Pueblo, *Myers s.n.* (F). KANSAS: Barber Co., Medicine Lodge, *Smyth 292* (NY, US). Barton Co., Pawnee Rock, *Lowell 45* (GH). Clark Co., *Hitchcock s.n.* (KSC). Edwards Co., *Hitchcock s.n.* (KSC). Finney Co., 0.5 mi S of Garden City, *McGregor 2183* (KSC). Gray Co., *Hitchcock s.n.* (KSC). Hamilton Co., S of Kendall, *Gates 16091* (KSC, WIS). Kearney Co., S of Lakin, *Anderson 2585* (DS, FSU). Kiowa Co., near Belvidere, *Ward s.n.* (GH, US). Marion Co., *Norton s.n.* (KSC). Meade Co., below Lake Larrabee, *Horr 3659* (US). Reno Co., near Sylvia, *Brownlee s.n.* (KSC). Rice Co., Sterling, *Anderson 2810* (FSU). Sedgwick Co., Wichita, *Smyth 735* (NY). Seward Co., Cimarron River bottom, *Gates 16245* (KSC). Shawnee Co., Topeka, *Smyth s.n.* (KSC). Stafford Co., 6 mi E of Hudson, *McGregor 13692* (F, NY). Wyandotte Co., Argentine, *MacKensie 1307* (K, KSC, MO, NY). MISSOURI: Jackson Co., Courtney, *Bush 8190* (GH, NY, US). Marion Co., Hannibal, *Davis 3249* (MO). NEW MEXICO: Bernalillo Co., along the Rio Grande, *Palmer 31131* (GH). Chaves Co., Lake Van, 1.4 mi SE of Dexter, *Pinkava et al. 3092* (ASU). Colfax Co., Cimarron River, *Fendler 536* (GH, K, MO, UC). Doña Ana Co., 9 mi N of Las Cruces, *Munz 13271* (LL, TEX, UC). Eddy Co., Carlsbad, *McKechnie 553* (MO). Guadalupe Co., Santa Rosa, *Dittmer 8479* (NMU). Sandoval Co., Bernalillo, *Arsène 19440* (F, LL, TEX, US). Socorro Co., Rio Grande bottom, *Ferris 1176* (DS). Valencia Co., near Belen, *Anderson 3229* (FSU). OKLAHOMA: Alfalfa Co., *Carleton 505* (US). Beckham Co., near Sayre, *Goodman 2352* (CAS, MO, NY). Blaine Co., 3 mi W of Watonga, *Waterfall 2386* (GH, NY). Canadian Co., flood plain of the Canadian River, *Waterfall 2506* (ARIZ). Cleveland Co., Norman, *Emvig 526* (US). Ellis Co., near Shattuck, *Stevens 2722* (GH). Harmon Co., near Hollis, *Stevens 1113* (DS, GH, NY). Harper Co., 20 mi E of Buffalo, *Smith 123* (TEX). Woods Co., near Alva, *Stevens 2808* (DS, GH, MO, US). Woodward Co., Woodward, *Locke 54* (US). TEXAS: Bailey Co., Coyote Lake, *Ferris & Duncan 3463* (CAS, DS, NY). Baylor Co., Seymore, *Reverchon 506* (NY, US). Childress Co. (TEX). Culberson Co., Rustler Springs, *Cory 2763* (GH). Dallam Co., Mustang Spring, *Havard 13* (NY, US). Donley Co., Lelia Lake, *Whitehouse 17260* (GA, MICH, NY, UC). Garza Co., Post, *Palmer 14574* (MO). Hemphill Co., Canadian River, *Rowell 5838* (TEX). Hockley Co., *Hams 47* (US). Howard Co., near Big Spring, *Reverchon 13* (GH). Hutchinson Co., Canadian River breaks, *Drake 173* (TEX). Lubbock Co., near Lubbock, *Reed 3145* (US). Motley Co., Roaring Springs, *Cory 16097* (TEX). Wheeler Co., N fork Red River, *Tharp & Tyson s.n.* (TEX). Wilbarger Co., near Vernon, *Eggert s.n.* (MO). UTAH: Grand Co., lower Courthouse Wash, near Colorado River, Arches Natl. Monument, *Welsh & Moore 2751* (NY, WIS).

Flaveria campestris is characterized by its annual habit, linear-lanceolate leaves with serrate or spinulose-serrate margins, contracted but not completely glomerulate capitulescence, 3-keeled phyllaries, 5–6(–8) florets per head, and distribution. The larger heads, less contracted capitulescence, and habit of *F. campestris* suggest that the taxon might have originated as an early, north-migrating offshoot of *F. bidentis*.

The localized distribution of *F. campestris*, restricted by saline and at least seasonally wet conditions, evidently fluctuates considerably from year to year. In Kansas, Anderson (1972) was not able to recollect from an exact site after six years. I have visited numerous precise localities of previous collections without finding the plants. In 1928 *F. campestris* was collected at Rustler Springs (*Cory 2763*), a permanently wet site in the gypsum plains of Culberson Co., Texas. When I visited the site in 1976, both *F. trinervia* and *F. chloraefolia* were abundant, but *F. campestris* was absent.

15. **Flaveria trinervia** (Spreng.) C. Mohr, Contr. U.S. Natl. Herb. 6: 810. 1901. TYPE: Botanical Garden, Halle, cultivated (not seen).

Oedera trinervia Spreng., Bot. Gard. Halle 63. 1800.
Brotera contrayerba Spreng., J. Bot. Schrad. 1800. *pl.* 5. 1801, non *Flaveria contrayerba* Pers., 1807.
Nauenbergia trinervata Willd., Sp. Pl. 3: 2393. 1804.
Brotera trinervata Pers., Syn. Pl. 2: 498. 1807.
Flaveria repanda Lag., Gen. & Sp. Nov. 33. 1816. TYPE: Mexico (not seen).
Brotera sprengelii Cass., Dict. Sci. Nat. 34: 306. 1825.
Flaveria trinervata Baillon, Hist. Pl. 55. 1882.

Plants delicate or robust annuals, 15–80 cm to more than 2 m high and nearly as broad, the stems often purplish, essentially glabrous; leaves opposite, 3–15 cm long, (0.7–)1–4 cm wide, essentially glabrous, lanceolate, oblanceolate, to elliptic or subovate, the margins serrate, serrate-dentate, or spinulose-serrate, the petioles of the main leaves 1–2 cm long, the petiole bases nearly connate, the blades of the upper leaves usually connate; capitulescence of glomerulelike, tightly clustered secondary heads, 1–2.5 cm wide, sessile, axillary, subtended by smaller cauline leaves; receptacles of glomerules with long, slender, membranous, chafflike setae; heads radiate or discoid, the florets usually 1, rarely 2; radiate heads mostly peripheral in glomerules; involucres 3.8–4.5 mm long, oblong and cylindrical or angular, the phyllaries usually 2, concave and rounded apically, closely investing and falling with mature achenes; ray corollas short, ca. 1.5 mm long, seemingly vestigial, pale yellow or whitish, the ligule barely protruding from the closed bracts, the ligule oblique or suborbicular, 0.5–1 mm long; disc corollas 2–2.5 mm long, the tubes 0.5–1.4 mm long, pubescent, the throats, 0.5–0.8 mm long, pubescent, campanulate, the lobes ca. 1 mm, acute; anthers ca. 1 mm long; achenes 2–2.6 mm long, oblanceolate or subclavate, the ray achenes longer; pappus absent; chromosome number, $n = 18$.

A weedy species even more widespread than *F. bidentis*, in a variety of habitats, usually saline, gypseous, and disturbed, usually near ephemeral or permanent water sources; throughout most of Mexico; Texas to Arizona in the United States, and other scattered localities, including Hawaii; Central America, British Honduras; Brazil, Ecuador, Peru, and Venezuela of South America, seemingly not in competition with *F. bidentis*; West Indies (Fig. 7); Africa; India; Middle East.

REPRESENTATIVE SPECIMENS: MEXICO. AGUASCALIENTES: Aguascalientes, *McVaugh & Rzedowski s.n.* (MICH, MO). CAMPECHE: Champotón, *King 6855* (MO, US). CHIAPAS:

Near Soyatitán, *Ton 3138* (MICH, NY). CHIHUAHUA: 3 mi W of Camargo, *Powell & Tomb 2658* (TEX, US). COAHUILA: 4 mi N of Monclova, *Flyr 239* (TEX). DISTRITO FEDERAL: San Angel, *Smyth 91* (US). DURANGO: Vicinity of Durango, *Palmer 481* (MO, NY, UC, US). GUANAJUATO: Near San Miguel Allende, *Kenoyer 2175* (GH). GUERRERO: Coyuca, *Hinton 7284* (GH, K, MICH, NY, UC). HIDALGO: Near Ixmiquilpan, *Quintero 2832* (DS, MICH, TEX). JALISCO: 4.5 mi W of Juanacatlán, *McVaugh 22089* (LL, MICH, NY, TEX). MORELOS: 10 mi NW of Cuantla, *Lyons 147* (MICH). NUEVO LEÓN: Laguna de Labradores, *Chase 7707* (ARIZ, F, GH, MICH, MO, NY). OAXACA: 1 mi N of Tamazulapan, *King 2937* (DS, MICH, NY, TEX, UC, US). QUERETARO: Cerro de las Campanas, *Arsène 10063* (F, MO, US). SAN LUIS POTOSÍ: Matehuala, *Shreve 8703* (ARIZ, MICH). SONORA: Magdalena, *Drouet & Richards 3799* (F). TAMAULIPAS: Vicinity Tampico, *Palmer 57* (CAS, F, GH, MO, NY, US). TLAXCALA: Hueyotlipan, *Nicolas s.n.* (GH). VERACRUZ: Veracruz, *Muller 150* (NY). YUCATÁN: Progreso, *Millspaugh 1653* (F). ZACATECAS: Hacienda de Cedros, *Lloyd 168* (US).

UNITED STATES. ARIZONA: Greenlee Co., Duncan, *Davidson 391* (GH). FLORIDA: Dade Co., Miami, *Burch 54* (GH). HAWAII: Oahu, *Egler 37-232* (LL, UC, US). MASSACHUSETTS: Middlesex Co., *Fletcher s.n.* (GH). MISSOURI: St. Louis Co., *Sherff 797* (F). NEW MEXICO: Chaves Co., 20 mi S of Roswell, *Earle & Earle 304* (K, MO, NMSU, NY, US). TEXAS: Culberson Co., 25 mi W of Orla, *Powell 2221* (TEX).

BELIZE. BELIZE: *Lundell 1884* (MICH, TEX, US).
BRAZIL. GOIÁS: Brasilia, *Riedel 938* (K).
ECUADOR. *Eggers 15704* (K).
PERU. CARAVELI: Near Lima, *Hutchinson 1293* (UC).
VENEZUELA. DISTRITO FEDERAL: Near Caracas, *Alston 5247* (NY, US).
BAHAMA ISLANDS. Great Inagua Island, *Dunbar 135* (A).
CUBA. LA HABANA: Near Havana, *Curtiss 545* (F, GH, MO, NY, US).
JAMAICA. Rose Hall, *Proctor 35286* (MO).
PUERTO RICO. *Liogier 10883* (GH, US).
ETHIOPIA. Harar, *Burger 1313* (US).
KENYA. Kisumu, *Tweedie 2358* (K).
RHODESIA. Salisbury, *Whellan 1845* (K).
SOMALIA. Northwest, *Gillett 4552* (K).
TANZANIA. Zanzibar, *Vaughan 1707* (K).
ZAMBIA. Monze, *Fanshawe 6873* (K).
MASCARENE ISLANDS. Mauritius, *Collector* (K).
INDIA. Tamil Nadu, *Gamble 16429* (K).
IRAQ. Baghdad, *Agnew 1867* (K).
SAUDI ARABIA. *Smith & Lavranos 33* (K).
YEMEN. *Woodford 1* (K).

Flaveria trinervia is perhaps the most derived species in the genus, along with the closely related *F. australasica*, in that many of the floral features are reduced from those which characterize the supposedly ancestral *F. bidentis* lineage. In *F. trinervia*, and *F. australasica*, the heads are very tightly aggregated into axillary glomerules, obviously in *Flaveria* a type of reduced capitulescence. Additionally the phyllaries are reduced to 2, there are 1(–2) florets per head, and the ligules are usually less than 1 mm long.

16. **Flaveria australasica** Hook., in Mitchell's J. Exped. Trop. Australia. 118. 1848. TYPE: Australia, Banks of Balook, subtropical New Holland, 6 Apr. 1846, *T. L. Mitchell 100* (K, lectotype).

Plants delicate or robust annuals, 15–80 cm to more than 2 m high, essentially glabrous; leaves opposite, 2–10 cm long, 0.4–1.3 cm wide, lanceolate, the margins serrate, serrate-dentate, or spinulose-serrate; capitulescence of axillary glomerules; receptacles of glomerules with long, slender, membranous, chafflike setae; heads radiate or discoid, florets usually 1, rarely 2; involucres 3.8–5 mm long, the phyl-

laries usually 2; ray florets with the ligule barely protruding from the closed bracts, 0.5–1 mm long; disc corollas 2–2.5 mm long; achenes (2.3–)2.5–4.5 mm long; chromosome number, $n = 18$.

Often in saline conditions, near rivers, streams, drainage canals, cultivated areas, or in coastal dune sand, Australia; distribution not mapped; flowering April–September.

REPRESENTATIVE SPECIMENS: AUSTRALIA. NEW SOUTH WALES: 50 mi N of Broken Hill, *Norris 2478* (NY). Mt. Browne, *Prayer 20833* (CAS). NORTHERN TERRITORY: E of Mataranks, *Blake 17512* (K). Victoria River, *Mueller s.n.* (GH, K). Brickerton Island, *Specht 536* (US). QUEENSLAND: 10 mi SE of Roma, *Johnson 2073* (K). Darling Downs, *Norman s.n.* (K). SOUTH AUSTRALIA: Flinders Range, *Koch s.n.* (K). WEST AUSTRALIA: Ashburton River, *Morrison s.n.* (K). Kimberly District, *Mueller s.n.* (NY). Monte Bello Island, *Purry 4* (K). Gascoyne Jnct., *Turner 5404* (TEX).

Flaveria australasica is exceedingly close to *F. trinervia* and probably is of only recent derivation from an Australian founder of the latter species. The taxa are so similar morphologically that when attempting to identify herbarium specimens, reference to distribution is often the most reliable method. In fact, it might be acceptable to recognize the Australian population as a variety of *F. trinervia*. Living greenhouse specimens of *F. australasica*, however, are readily distinguished from *F. trinervia* by their taller, more slender habit and narrower, lanceolate leaves. The Australian plants also exhibit slightly longer involucres, somewhat thicker phyllaries, slightly larger disc corollas, and longer achenes.

17. **Flaveria palmeri** J. R. Johnston, Proc. Amer. Acad. Arts 39: 290. 1903. TYPE: Mexico, Coahuila, San Lorenzo de Laguna, 94–114 km SW of Parras, 1–10 May 1880, *E. Palmer 684* (GH, holotype; F, K, NY (2), US, isotypes).

Plants delicate or robust annuals (5–)10–75 cm high, to 0.5–1 m wide, glabrous or sparsely pilose, or tufted, especially in the axils; leaves opposite, often appearing whorled, 3–8 cm long, 0.4–1.4 cm wide, essentially glabrous, lanceolate to broadly so, or linear, weakly serrate, sessile or subsessile; capitulescence of tightly aggregated heads extended alternately on very short, modified peduncles giving a subscorpioid effect; heads radiate or discoid, the radiate heads mostly peripheral; involucres 4–5 mm long, 1–2 mm wide, cylindrical to suboblong and somewhat flattened or angular, the phyllaries 3(–4), ovate-lanceolate or elliptic, boat shaped, the apex minutely lacerate, rounded or obtuse; calyculate bracts 1–2 linear, ca. 2 mm long; ray florets with the ligules yellow, ca. 2 mm long, ovate to orbicular, notched; disc florets (3–)5–8, the corollas 2.5–3 mm long, the tubes 0.8–1 mm long, the throats 1.2–1.5 mm long, narrowly funnelform, 0.4–0.5 mm long, acute; anthers ca. 1.8 mm long; achenes (1.7–)2–2.5(–2.8) mm long, those of the ray florets longer (by 0.5 mm), narrowly oblanceolate to linear; pappus absent; chromosome number, $n = 18$.

Gypsum flats and knolls, or clay-loam soils probably with dilute gypsum, bolsons near lagunas, distributed areas near roads and fields, mostly in south-central Coahuila (Fig. 2).

REPRESENTATIVE SPECIMENS: MEXICO. COAHUILA: 76.3 mi W of Cuatro Ciénegas, *Bacon & Leverich 1168* (TEX). 3 mi E of Torreón, *Fisher 44151* (CAS, GH, MO, NY). Near Matri-

monio Sta., *Johnston 9373* (GH, LL, TEX). Rancho Acatita, *McGill & Keil 8054* (ASU). Puerto Salada, *Pinkava et al. 5439* (ASU). Just SW of Cuatro Ciénegas, *Powell & Tomb 2621* (TEX, US). 39 mi N of San Pedro, *Powell & Tomb 2611* (TEX, US). Just N of Matamoros, *Sikes et al. 838* (TEX, US). 15 mi E of Cuatro Ciénegas, *Sikes et al. 851* (TEX, US). Laguna del Rey, *Stewart & Santos 3021* (GH). 25 mi W of El Oro, *White 2020* (ARIZ, GH, MICH, US). 25 mi E of Americanos, *Wynd 755* (ARIZ, GH, K, US). NUEVO LEÓN: Monterrey, *Arsène 10090* (US).

The distinctive annual, *F. palmeri*, a C_4 species commonly found between Torreón and Cuatro Ciénegas, Coahuila, is probably an early offshoot of the *F. bidentis* line. In overall morphology, phyllary number, and floret number, *F. palmeri* is similar to *F. bidentis* and *F. campestris*, but the former species differs in its self-incompatibility, usually narrower leaves, more open capitulescence, and in several floral traits. *Flaveria palmeri* is most closely related to *F. intermedia*. Both *F. trinervia* and *F. chloraefolia* occur sporadically within the range of *F. palmeri*, but these taxa are evidently ecologically and reproductively isolated.

18. **Flaveria intermedia** J. R. Johnston, Proc. Amer. Acad. Arts 39: 287. 1903. TYPE: Mexico, Durango, plains near Yermo, 17 Oct. 1896, *C. G. Pringle 7359* (GH, holotype; F, US, isotypes).

Plants erect annuals, 16–25 cm high, glabrous or sparsely pilose, tufted in the axils; leaves opposite, sessile, 2–4 cm long, 2–4.5 mm wide, essentially glabrous, lanceolate or linear, weakly serrate; capitulescence of tightly aggregated heads, giving a subcorymbose effect; heads radiate or discoid; involucre ca. 4 mm long, oblong-angular, the phyllaries 3, ovate-elliptic; ray florets with the ligules 1.5–2 mm long, ovate-elliptic, notched or acute; disc florets 5, the corollas 2–2.9 mm long, the tubes ca. 1 mm long, the throats ca. 1 mm long, tubular below, abruptly expanding to broadly funnelform or campanulate above, the lobes acute; achenes of the disc florets ca. 2 mm long, the ray achenes 2.8–3 mm long, narrowly oblanceolate to linear; pappus absent; chromosome number, unknown.

Known only from the type locality (Fig. 2).

Flaveria intermedia is exceedingly close to *F. palmeri* and the two might eventually be considered as conspecific. Here I have retained *F. intermedia* as a species because it is known only from the disjunct type locality, and because several minor character differences are exhibited in the collection. In describing both *F. intermedia* and *F. palmeri*, Johnston (1903) failed to note their close relationship. *Flaveria intermedia* differs from *F. palmeri* in the following traits: usually smaller habit; usually smaller leaves; shorter phyllaries; shorter ligules, acute or notched at the apex; shorter achenes; and perhaps most conspicuously, the basally tubular disc corollas are expanded distally to a broadly tubular-campanulate throat. During field studies I was not able to relocate *F. intermedia* in the type locality vicinity, and it is possible that the plant is no longer extant.

19. **Flaveria anomala** B. L. Robinson, Proc. Amer. Acad. Arts 27: 178. 1892. TYPE: Mexico, San Luis Potosí, plains, Vanegas, Sept. 1890, *C. G. Pringle 3669* (GH, lectotype; F, isolectotype). San Luis Potosí, in route from San

Luis Potosí to San Antonio, Texas, Aug. 1878, *C. C. Parry 500* (F, GH, MICH, NY, syntypes).

Plants delicate or robust annuals, (6–)15–75 cm high, to 0.5–1 mm wide, the stems rather lax or densely clumped, often purplish, essentially glabrous except with tufted hairs in the axils; leaves opposite, sessile, 3.5–10 cm long, 0.2–1 cm wide, glabrous, linear, lanceolate, or oblanceolate, the margins entire and subundulate or weakly serrate; capitulescence of tightly aggregated heads, with several clusters exhibiting a corymbose effect, the central heads discoid, the peripheral heads uniligulate, giving the effect of a single radiate, composite head; involucres 2.5–4.5 mm long, including the beaked apices, the phyllaries 2–3(–4), boat shaped and beaked, at maturity one or all swollen and corky below the beaks, the gibbous phyllaries also often winged, each phyllary enclosing an achene or not, the whole involucre closely investing and falling with the achenes; ray florets with the ligules 3.5–5 mm long, 2–3 mm wide, elliptical, rounded or emarginate at the apices; disc florets usually 1, often 2, rarely 3, the corollas 2.5–3 mm long, the tubes ca. 1 mm long, the throats 1–1.2 mm long, abruptly expanded into a funnelform campanulate shape, the lobes ca. 0.5 mm long, acute; anthers ca. 1.2 mm long; achenes 1.3–2.2 mm long, those of the ray florets larger and longer by 0.2–0.4 mm, narrowly oblanceolate to linear; pappus absent; chromosome number, $n = 18$.

High gypsum plains, often in disturbed sites, desert scrub or pine forests, 1,500–2,100 m, southern Coahuila south to Zacatecas and San Luis Potosí, east to Tamaulipas where plants may occur at 50 m elevation (Fig. 2).

REPRESENTATIVE SPECIMENS: MEXICO. COAHUILA: 6 mi N of La Ventura, *Johnston 7647* (CAS, GH). 26.5 mi N of Concepción del Oro, *Powell & Tomb 2599* (TEX, US). NUEVO LEÓN: 8 mi S of Galeana, *Correll & Johnston 19867* (TEX). 7.5 mi S of San Roberto Jnct., *Powell & Tomb 2559* (TEX, US). 34.4 mi S of San Roberto Jnct., *Powell & Tomb 2566* (TEX, US). 40 mi N of Matehuala, *Waterfall 15757* (F). SAN LUIS POTOSÍ: 9 mi NW of Ciudad Maíz, *Graham & Johnston 4473* (TEX). 1 mi N of Matehuala, *Powell & Tomb 2568* (TEX, US). Presa de Guadalupe, *Rzedowski 6755* (MICH). Near Salado, *Shreve 9354* (ARIZ, GH, MICH, UC). TAMAULIPAS: 0.5 mi S of Santander Jiménez, *Graham & Johnston 4818* (MICH, TEX). 4 mi S of Jaumave, *Stanford et al. 2227* (CAS, DS, MICH, NY, UC, US). ZACATECAS: 8.5 mi NE of Concepción del Oro, *Powell & Tomb 2594* (TEX, US). Sierra Hermosa, *Shreve 8591* (ARIZ, MICH, US).

The most distinctive features of *F. anomala* include the boat-shaped, beaked phyllaries which at maturity may become swollen and corky basally, closely investing and falling with the fruit; usually 1(–3) flower per head. Also, in *F. anomala* the radiate heads (each with a conspicuous ligule) have peripheral arrangement in the capitulescence clusters, and more than any other *Flaveria* thus display the effect of a typical radiate composite head.

Flaveria anomala and its related species *F. ramosissima* are the only annual taxa of the genus with C_3 metabolism. The morphologies of these species suggest that they are of ancestry similar to that of the C_4 annual species, which means that *F. anomala* and *F. ramosissima* were perhaps derived from the C_3 *F. angustifolia* line (Fig. 1).

The weedy *F. trinervia* grows intermixed with *F. anomala* throughout much

of its range, but without any apparent hybridization. Experimental data (Table 1) suggest that the two distinct taxa are reproductively isolated. The ranges of *F. anomala* and *F. palmeri* are proximal but spatially isolated (Fig. 2) at present. Experimental data (Table 1) indicate that the *F. anomala* and *F. palmeri* are so strongly isolated reproductively that hybridization could not succeed if future distributional changes should bring them into contact. Indeed, the two contiguous annual species probably evolved strong reproductive barriers in response to characteristic *r*-selection strategy (Gadgil & Solbrig, 1972).

20. **Flaveria ramosissima** Klatt, Leopoldina 23: 146. 1887. TYPE: Mexico, Puebla, Tehuacán, *Liebmann 456* (K, lectotype; GH, isolectotype, fragment). *Liebmann 457* (K, US, paratypes, on the sheet with *Liebmann 456*).

F. angustifolia Schultz Bip. ex Klatt var. *ramosissima* Klatt, Leopoldina 23: 146. 1887.

Plants annual, 12–50 cm high, erect, the stems diffuse, often purplish, glabrate to sparsely hairy below, becoming sparsely villous above; leaves opposite, connate, 2.5–5 cm long, 0.2–0.6 cm wide, glabrous, linear or linear-lanceolate, entire or minutely serrate; capitulescence of numerous heads rather tightly aggregated in subscorpioid, corymbiform clusters; heads radiate or discoid; involucres ca. 3 mm long, angular-urceolate, the phyllaries 5, oblong-ovate or boat shaped; calyculate bract 1, linear, ca. 1 mm long; ray florets with the ligules ca. 3 mm long, 1.5–2 mm wide, oblong-orbicular; disc florets 5–8(–10), the corollas ca. 2 mm long, the tubes 0.6–0.7 mm long, the throats 0.7–0.9 mm long, funnelform, the lobes ca. 0.5 mm long, acute; anthers ca. 1 mm long; ray achenes 1.3–1.5 mm long, the disc achenes ca. 1 mm long, oblanceolate or linear; pappus absent; chromosome number, $n = 18$.

Sandy-clay bottoms, along dry washes, fields and roadsides, possibly in gypseous soils, thorn-scrub vegetation, 800–1,700 m, Tehuacán Valley area, Puebla and Oaxaca, Mexico (Fig. 3).

REPRESENTATIVE SPECIMENS: MEXICO. OAXACA: 12 km SSE of Teotitlán, *Cronquist 11235* (MO, US). PUEBLA: 8 mi SE of Coxcatlán, *Anderson & Anderson 5340* (MICH). 2.5 mi NW of Teotitlán, *Cronquist & Sousa 10381* (CAS, GH, MICH, NY, TEX, US). Tehuacán, *Matuda 32279* (US).

This annual species is characterized by its diffuse, low branching habit, narrow leaves, rather open, somewhat scorpioid capitulescence, showy radiate heads with ligules 3 mm long, small achenes and disc corollas, and distribution. *Flaveria ramosissima* probably has affinity with the *F. angustifolia* line, but seems more closely related to *F. anomala*, also a C_3 species.

21. **Flaveria mcdougallii** Theroux, Pinkava & Keil, Madroño 24: 13. 1977. TYPE: United States, Arizona, Mohave Co., Grand Canyon National Park, Cove Canyon (174.2 mi below Lee's Ferry), 27 Jan. 1976, *M. E. Theroux 1675* (US, holotype; ARIZ, ASC, ASU, DES, GCNP, GH, MNA, NY, RSA, SRSU, TEX, UC, isotypes).

Plants suffrutescent, ca. 50 cm high, the stems erect, glabrous; leaves opposite, weakly connate basally, 5–11 cm long, 2–7 mm wide, glabrous, linear-lanceolate,

the margins entire; capitulescence corymbose, with the heads arranged in several small clusters; heads discoid; involucres turbinate, ca. 3 mm long, the phyllaries 2–6, oblong, 2–3 mm long, ca. 0.7 mm wide; calyculate bracts 1–2 mm long; disc florets 2–6, the corollas 3.5 mm long, exserted conspicuously from the involucre, the tubes ca. 1 mm long, the throats 1.5 mm long, the lobes ca. 1 mm long; achenes ca. 1.5 mm long, linear; pappus a crown of fringed scales, ca. 0.3 mm long; chromosome number, $n = 18$.

Known only from near saline springs at the mouths of two remote tributary canyons in the Grand Canyon (Theroux et al., 1977), (Fig. 2).

PARATYPES: UNITED STATES. ARIZONA: Coconino Co., Grand Canyon National Park, Matkatamiba Canyon (148.8 mi below Lee's Ferry), 1 Oct. 1975, *M. E. Theroux 1519* (MNA). Mohave Co., Grand Canyon National Park, Cove Canyon, 5 Oct. 1975, *M. E. Theroux 1567* (MNA).

Flaveria mcdougallii was thoroughly discussed by Theroux et al. (1977). The delimiting characters of this species include: linear leaves with entire margins; 2–6 phyllaries; discoid heads with 2–6 florets; glabrous corollas; achenes with (or without) double hairs; pappus crown of scales; and distribution. The morphological and experimental data accumulated so far suggest that *F. mcdougallii* might well stand alone as a monotypic genus (see Hybridizations). For the present, however, I prefer to retain the species in *Flaveria* while additional studies are conducted, particularly crosses with additional species of *Flaveria*.

EXCLUDED SPECIES

For a list of excluded species see Rydberg, 1915.

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INDEX OF LATIN NAMES

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CHROMOSOME NUMBERS OF TROPICAL AMERICAN GRASSES (GRAMINEAE): 5[1,2]

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ABSTRACT

Chromosome numbers and meiotic behavior are reported in 101 collections of grasses representing 42 genera and 85 species. First chromosome reports are given for the following 21 species: *Agrostis turrialbae*, $n = 14$; *Andropogon hypogynous*, $n = 30$; *Axonopus pruinosus*, $n = 30$; *Aristida riparia*, $n = 11$; *A. setifolia*, $n = 11$; *A. torta*, $n = 11$; *A. venesuelae*, $n = 22$; *Chusquea scabra*, $n = 20$; *Festuca chiriquensis*, $n = 14$; *Gymnopogon spicatus*, $n = 10$; *Muhlenbergia lehmanniana*, $n = 10 + 2B$; *Olyra lateralis*, $n = 18$; *Panicum guianense*, $n = 20$; *P. macranthum*, $n = 27$; *P. olyroides*, $n = 18$; *P. pyrularium*, $n = 18$; *Paspalum gardnerianum*, $n =$ ca. 20; *Pereilema brasilianum*, $n = 20$; *Stipa hans-meyeri*, $n = 11$; *Swallenochloa longiligulata*, $n = 20$; *Swallenochloa weberbaueri*, $n = 20$. Counts differing from previously reported numbers are given for the following 5 species: *Axonopus fissifolius*, $n = 30$; *Pappophorum pappiferum*, $n = 50$; *Paspalum carinatum*, $n = 10$; *P. minus*, n = 25; *Pennisetum setosum*, $n = 18$.

This paper is a continuation of our earlier studies on the chromosome numbers of tropical American grasses (Pohl & Davidse, 1971; Davidse & Pohl, 1972a, 1972b, 1974). Tropical America continues to be one of the most poorly studied areas in the world in terms of known chromosome numbers of grasses. We intend to continue to provide basic information concerning chromosome numbers and meiotic behavior of tropical American grasses as this becomes available.

Since our review of important contributions dealing with chromosome numbers of tropical American grasses (Davidse & Pohl, 1974), several other papers have been published: Moraes Fernandes et al. (1974), Koch (1974), Hickenbick et al. (1975), and Quarin (1977).

All chromosome counts were made from squashes of microsporocytes. The methods used are those noted in Davidse & Pohl (1972a). Vouchers for the Pohl and the Pinette specimens are deposited in the Iowa State University Herbarium (ISC), and for the Davidse specimens in the Missouri Botanical Garden Herbarium (MO). Voucher slides are available for most of the counts at MO.

RESULTS AND DISCUSSION

A complete list of the species studied, their chromosome numbers, and the voucher specimens is given in Table 1. Two asterisks (**) after a number indi-

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[1] Journal Paper No. J-9033 of the Iowa Agriculture and Home Economics Experiment Station, Ames, Project 1833.

[2] Part of the field work was supported by N.F.S. grants DEB 73-00834 A01 to Davidse and GB-32085 to Pohl. We would like to thank Dr. Enrique Forero, Bogotá for his assistance with the Colombian field work, and Dr. Tobias Lasser, Dr. Julian A. Steyermark, Dr. Stephen S. Tillett, and Mr. Gilberto Morillo, all of Caracas, for assistance with the Venezuelan field work.

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ANN. MISSOURI BOT. GARD. 65: 637–649. 1978.

0026-6493/78/0637–0649/$01.45/0

cate that the count is the first for the species; one asterisk (*) indicates that the count differs from any previous one for the same species. The collections are arranged alphabetically by genus and species under their respective subfamilies. Unless otherwise indicated in the text, meiosis was normal for all collections listed in Table 1. New chromosome number determinations and some of those of irregular meiotic behavior or other special interest are illustrated in Figs. 1–30.

SUBFAMILY BAMBUSOIDEAE

The very similar genera *Chusquea* and *Swallenochloa* are here again shown (Figs. 1, 3–4) to have a basic chromosome number of $x = 10$ rather than $x = 12$ as was previously indicated by Janaki Ammal (1959) for three South American species of *Chusquea*. All other earlier counts (Pohl & Davidse, 1971; Davidse & Pohl, 1972b, 1974) have been based on Central American material, so it is important that we have been able to confirm this base number from South America for the first time with a count from *Swallenochola weberbaueri* (Fig. 3) of the Colombian páramos.

An aneuploid reduction series is characteristic of the genus *Olyra*. Base numbers previously known for this genus include: $x = 7$, *O. fasciculata* Trin. (Calderón & Soderstrom, 1973); $x = 10$, *O. micrantha* (Gould & Soderstrom, 1967; Davidse & Pohl, 1974, this paper), *O. taquara* Swallen (Gould & Soderstrom, 1967); $x = 11$, *O. latifolia* (Tateoka, 1962—fide Calderón & Soderstrom, 1973; Reeder et al., 1969; Pohl & Davidse, 1971; Davidse & Pohl, 1972a, 1972b, 1974, this paper; Kammacher et al., 1973; Olorode, 1975), *O. loretensis* Mez (Gould & Soderstrom, 1970), *O. obliquifolia* Steud. (Gould & Soderstrom, 1967). To the above numbers, we can now add a new base number of $x = 9$ for *O. lateralis* (Fig. 2), which is morphologically anomalous in *Olyra* and will probably be assigned to a new genus in the future. *Olyra cordifolia* H.B.K. has been reported by Gould and Soderstrom (1967) to have $2n = 30$. It would be very desirable to make further counts of *O. cordifolia* to determine whether this count represents a triploid based upon $x = 10$, or, more likely, an aneuploid secondarily derived from a polyploid. Once the genus is better known cytologically, it may be possible to correlate different base numbers and ploidy levels with at least some of the myriad of morphological types in the genus. Our collection of *O. micrantha* showed occasional chromosome bridges, but no other irregularities.

SUBFAMILY POOIDEAE

Calamagrostis intermedia, $n = 28$, consistently formed one to five quadrivalents at diakinesis (Fig. 6). Previously, we (Pohl & Davidse, 1971) determined the same number for another Costa Rican collection and noted other irregularities, bridges and laggards—but not multivalents—at metaphase and anaphase I.

SUBFAMILY CHLORIDOIDEAE

Muhlenbergia lehmanniana (Fig. 14) had one or two B-chromosomes in most of the cells examined, although some cells clearly lacked them. These chromo-

TABLE 1. Chromosome numbers of tropical American grasses.

Species	*n*	Voucher
	Subfamily Bambusoideae	
Chusquea		
scabra Soders. & Cald.	20**	COSTA RICA. CARTAGO: 4 km NE of Capellades, *Pohl & Pinette 13305*. CARTAGO: 3 km W of Santa Cruz, *Pohl & Pinette 13307*.
Olyra		
lateralis (Presl) Chase	18**	PANAMÁ. PANAMÁ: Cerro Jefe, *Davidse & D'Arcy 10102*.
latifolia L.	22	VENEZUELA. BOLÍVAR: 17 km W of the Río Caura, *Davidse 4442*.
micrantha H.B.K.	20	VENEZUELA. BOLÍVAR: La Gran Sabana, KM 248, *Davidse et al. 4920*.
Pharus		
glaber H.B.K.	ca. 22	COSTA RICA. PUNTARENAS: Finca Las Cruces Botanical Garden, *Pohl & Lucas 13127*.
Swallenochloa		
longiligulata Soders. & Cald.	20**	COSTA RICA. SAN JOSÉ: Tres de Junio, *Pohl & Selva 12842, 12843*.
subtessellata (Hitchc.) McClure	20	COSTA RICA. SAN JOSÉ: 4.6 km NW of La Georgina, páramo, *Pohl & Lucas 13137*.
weberbaueri (Pilger) McClure vel sp. aff.	20**	COLOMBIA. CUNDINAMARCA: Between Bogotá and Choachí, *Davidse et al. 5527*.
	Subfamily Oryzoideae	
Luziola		
pittieri Luces	12	VENEZUELA. APURE: Ca. 30 km NE of Mantecal, *Davidse et al. 3828*.
Oryza		
latifolia Desv.	24	COSTA RICA. GUANACASTE: Cañas, Finca La Pacifica, *Pohl & Selva 12957*.
	Subfamily Arundinoideae	
Gynerium		
sagittatum (Aubl.) Beauv.	22	COSTA RICA. LIMÓN: Río Pacuare, 5 km NE Siquirres, *Pohl & Selva 12896*.
	Subfamily Pooideae	
Agrostis		
turrialbae Mez	14**	COSTA RICA. CARTAGO: 20.6 km S. of Empalme, *Pinette 1297*.
Calamagrostis		
intermedia (Presl) Steud.	28	COSTA RICA. SAN JOSÉ: 4.6 km NW of La Georgina, *Pohl & Lucas 13138*.
Cinna		
poaeformis (H.B.K.) Scribn. & Merr.	14	COSTA RICA. CARTAGO: Volcán Irazú, 2700 m, *Pohl & Selva 12875*.
Festuca		
chiriquensis Swallen	14**	PANAMÁ. CHIRIQUÍ: Ca. 9 km WNW of Boquete, *Davidse & D'Arcy 10312*.
Stipa		
hans-meyeri Pilger	11**	COSTA RICA. SAN JOSÉ: Cerro Buena Vista, *Pohl & Selva 12846*.
Trisetum		
tonduzii Hitchc.	14	COSTA RICA. CARTAGO: Volcán Irazú, above Sanitario Duran, 2700 m, *Pohl & Selva 12876*.

TABLE 1. (Continued)

Species	*n*	Voucher
		Subfamily Chloridoideae
Aristida		
capillacea Lam.	11	COLOMBIA. VICHADA: Ca. 8 km N of Las Gaviotas, *Davidse & Llanos 5148.*
recurvata H.B.K.	11	COLOMBIA. VICHADA: Ca. 8 km N of Las Gaviotas, *Davidse & Llanos 5134.*
riparia Trin.	11**	VENEZUELA. BOLÍVAR: 36 km E of the Río Cuchivero, *Davidse 4422.*
setifolia H.B.K.	11**	VENEZUELA. GUÁRICO: Estación Biológica de Los Llanos, *Davidse 2923.* GUÁRICO: 15 km S of Las Mercedes, *Davidse 4250.*
torta (Nees) Kunth s. lat.	11**	VENEZUELA. BOLÍVAR: La Gran Sabana, KM 287, *Davidse et al. 4911.*
venesuelae Henr.	22**	VENEZUELA. ANZOÁTEGUI: 6 km ESE of La Ceiba, *Davidse et al. 4519.*
Bouteloua		
williamsii Swallen	10	MEXICO. OAXACA: Ca. 12 mi NW of El Camarón, *Davidse & Davidse 9597.*
Eragrostis		
mexicana (Hornem.) Link	30	COSTA RICA. ALAJUELA: 3 km S of the Palmares exit, *Pohl & Lucas 12946.*
Eustachys		
petraea (Swartz) Desf.	20	MEXICO. VERACRUZ: 5 mi E of Coatzacoalcos, *Davidse & Davidse 9338.*
Gouinia		
latifolia (Griseb.) Vasey	40	VENEZUELA. BOLÍVAR: 21 km E of the Río Caura, *Davidse 4465.* COLOMBIA. CUNDINAMARCA: 14 km WNW of Melgar, *Davidse et al. 5794.*
Gymnopogon		
fastigiatus Nees	20	COLOMBIA. META: 73 km W of Las Gaviotas, *Davidse & Llanos 5400.*
foliosus (Willd.) Nees	10	VENEZUELA. BOLÍVAR: 28 km W of the Río Caura, *Davidse 4424.*
spicatus (Spreng.) Kuntze	10**	BRAZIL. DISTRITO FEDERAL: 3 km W of the Goias-Distrito Federal border on Highway BR 020-030, *Davidse et al. 12166.*
Muhlenbergia		
lehmanniana Henr.	10 + 2B**	PANAMÁ. CHIRIQUÍ: Ca. 3 km NE of El Hato del Volcán, *Davidse & D'Arcy 10332.*
setarioides Fourn.	20	COSTA RICA. CARTAGO: Between Llano Grande and Tierra Blanca, *Pohl & Lucas 13097.*
Pappophorum		
pappiferum (Lam.) Kuntze s. lat.	50*	VENEZUELA. ANZOÁTEGUI: 18 km W of El Tigre, *Davidse et al. 4976.* BOLÍVAR: 13 km ESE of Upata, *Davidse et al. 4615.*
Pereilema		
brasilianum Trin.	20**	BRAZIL. GOIAS: 18 km of Alvarada do Norte *Davidse et al. 12214.*
Sporobolus		
jacquemontii Kunth	12	COSTA RICA. PUNTARENAS: Paso Real, *Pohl & Selva 12847.*
virginicus (L.) Kunth	10	MEXICO. VERACRUZ: 5 mi E of Coatzacoalcos, *Davidse & Davidse 9339.*

TABLE 1. (Continued)

Species	*n*	Voucher
		Subfamily Panicoideae
Acroceras zizanioides (H.B.K.) Dandy	18	COLOMBIA. META: 20 km W of Puerto López, *Davidse & Llanos 5495.*
Andropogon hypogynous Hack.	30**	COLOMBIA. META: 2 km E of Puerto Gaitán, *Davidse & Llanos 5404.*
Axonopus capillaris (Lam.) Chase	20	VENEZUELA. GUÁRICO: Ca. 50 km N of San Fernando de Apure, *Davidse et al. 3824.*
fissifolius (Raddi) Kuhlm.	30*	VENEZUELA. BOLÍVAR: 35 km E of the Río Cuchivero, *Davidse 4421.*
pruinosus Henr.	30**	VENEZUELA. BOLÍVAR: 32 km N of La Ciudadella, *Davidse et al. 4955.*
Brachiaria fasciculata (Swartz) Parodi	9	COSTA RICA. GUANACASTE: Cañas, Finca La Pacifica, *Pohl & Selva 12958.*
Digitaria abyssinica (Hochst.) Stapf	18	COSTA RICA. HEREDIA: Alto de Roble, *Pohl & Lucas 13001.*
bicornis (Lam.) R. & S.	36	VENEZUELA. SUCRE: Cumaná, *Davidse 5022.* MEXICO. VERACRUZ: 5 mi E of Coatzacoalcos, *Davidse & Davidse 9345.*
ciliaris (Retz.) Koel	27	COSTA RICA. ALAJUELA: Near Palmares, *Pohl & Selva 12950.*
Echinolaena gracilis Swallen	10	COLOMBIA. META: 73 km W of Los Gaviotas, *Davidse & Llanos 5394.* VENEZUELA. GUÁRICO: Ca. 21 km SE of Calabozo, *Davidse 3739.*
Eriochloa punctata (L.) Desv.	18	VENEZUELA. GUÁRICO: Río Orituco, *Davidse 3719.*
Euclasta condylotricha (Hochst. ex Steud). Stapf	10	VENEZUELA. GUÁRICO: 10 km NWN of Altagracia de Orituco, *Davidse 4186.*
Homolepis aturensis (H.B.K.) Chase	10	MEXICO. TABASCO: 4 km W of Huimanguillo, *Davidse & Davidse 9365.*
Hymenachne amplexicaulis (Rudge) Nees	10	VENEZUELA. APURE: Near Mantecal, *Davidse et al. 3869.* COLOMBIA. META: 20 km W of Puerto López, *Davidse & Llanos 5496.*
Hypogynium virgatum (Desv. ex Hamilt.) Dandy	10	COLOMBIA. VICHADA: Ca. 51 km E of Las Gaviotas, *Davidse & Llanos 5239.*
Ichnanthus nemorosus (Swartz) Doell	ca. 20	COSTA RICA. HEREDIA: Alto de Roble, *Pohl & Lucas 13000.*
Isachne polygonoides (Lam.) Doell	10	VENEZUELA. GUÁRICO: Ca. 32 km SSE of Calabozo, *Davidse 3772.*
Ischaemum indicum (Houtt.) Merr.	10	COSTA RICA. LIMÓN: 2 km W of Bambu, *Pohl & Pinette 13195.*
rugosum Salisb.	9	VENEZUELA. GUÁRICO: 23 km NE of Chagauramas, *Davidse 4230.* GUÁRICO: ca. 50 km N of San Fernando de Apure, *Davidse et al.* 3822.

TABLE 1. (Continued)

Species	*n*	Voucher
Otachyrium versicolor (Doell) Henr.	10	VENEZUELA. APURE: 42 km NE of Mantecal, *Davidse et al. 3910.*
Panicum cordovense Fourn.	27	COSTA RICA. SAN JOSÉ: 21 km S of Cartago, *Pohl & Lucas 13004.*
glutinosum Swartz	20	PANAMÁ. PANAMÁ: Cerro Jefe, *Davidse & D'Arcy 10117.* MEXICO. CHIAPAS: Ca. 8 mi NE of Solistohuacan, *Davidse & Davidse 9446.* VENEZUELA. DISTRITO FEDERAL: Road to Carayaca, *Davidse & Morillo 4004.*
guianense Hitchc.	20**	VENEZUELA. GUÁRICO: Río Orituco, *Davidse 3716.*
laxum Swartz	20	COSTA RICA. GUANACASTE: Cañas, Finca La Pacifica, *Pohl & Selva 12959.*
macranthum Trin.	27**	BRAZIL. BAHIA: 15 km S of intersection of Highway BR-020 and Río Roda Velha, *Davidse et al. 12085.*
mertensii Roth.	20	COLOMBIA. META: 20 km W of Puerto López, *Davidse & Llanos 5500.*
olivaceum Hitchc. & Chase	9	PANAMÁ. CHIRIQUÍ: Ca. 9 km WNW of Boquete, *Davidse & D'Arcy 10308.*
olyroides H.B.K.	18**	COLOMBIA. VICHADA: Ca. 8 km N of Las Gaviotas, *Davidse & Llanos 5132.*
parvifolium Lam.	18	COLOMBIA. META: 73 km W of Las Gaviotas, *Davidse & Llanos 5401.*
pilosum Swartz	10	COLOMBIA. CAQUETÁ: 23 km N of Florencia, *Davidse et al. 5760.*
pyrularium Hitchc. & Chase	18**	COLOMBIA. META: 14 km NW of Villavicencio, *Davidse & Llanos 5518.*
rudgei R. & S.	9	COLOMBIA. META: 43 ENE of Puerto López, *Davidse & Llanos 5106.* COSTA RICA. PUNTARENAS: Savannas of Buenos Aires, *Pohl & Lucas 13116.*
sphaerocarpum Ell.	9	PANAMÁ. CHIRIQUÍ: E slope of Volcán de Chiriquí, *Davidse & D'Arcy 10153.*
trichanthum Nees	18	COSTA RICA. LIMÓN: Cahuita, *Pohl & Selva 12914.*
trichoides Swartz	9	VENEZUELA. GUÁRICO: 15 km SW of Tamaco, *Davidse 4213.*
Paspalum botterii (Fourn.) Chase	40	COSTA RICA. GUANACASTE: Hacienda Paloverde, *Pohl & Selva 12938.*
carinatum Humb. & Bonpl. ex Flügge	10*	VENEZUELA. BOLÍVAR: 31 km W of Caicara, *Davidse 4366.*
decumbens Swartz	10	COLOMBIA. CAQUETÁ: 23 km N of Florencia, *Davidse et al. 5761.*
gardnerianum Nees	ca. 20**	COLOMBIA. VICHADA: Ca. 10 km W of Las Gaviotas, *Davidse & Llanos 5360.*
minus Fourn.	25*	COSTA RICA. PUNTARENAS: 8 km E. of Esparza, *Pohl & Selva 12954.*
minus Fourn.	ca. 20	COLOMBIA. VICHADA: 31 km W of Las Gaviotas, *Davidse & Llanos 5378.*
multicaule Poir.	10	VENEZUELA. GUÁRICO: Ca. 32 km SSE of Calabozo, *Davidse 3773.* COLOMBIA. VICHADA: Ca. 8 km N of Las Gaviotas, *Davidse & Llanos 5127.*

TABLE 1. (Continued)

Species	*n*	Voucher
notatum Flügge	20	COSTA RICA. GUANACASTE: Cañas, Finca La Pacifica, *Pohl & Selva 12960.*
pectinatum Nees	10	COLOMBIA. VICHADA: Ca. 25 km E of Cumaribo, *Davidse & Llanos 5321.*
plicatulum Michx.	10	MEXICO. TABASCO: 4 km W of Huimanguillo, *Davidse & Davidse 9363.*
reclinatum Chase	30	COSTA RICA. CARTAGO: Canyon of Río Grande de Orosí, S of Tapantí, *Pohl & Selva 12882.*
virgatum L.	20	COSTA RICA. LIMÓN: 2 km W of Bambu, *Pohl & Pinette 13199.* MEXICO. TABASCO: 4 km W of Huimanguillo, *Davidse & Davidse 9356.*
Pennisetum		
setosum (Swartz) L. Rich.	18*	COLOMBIA. VICHADA: Ca. 35 km E of Las Gaviotas, *Davidse & Llanos 5194.*
setosum (Swartz) L. Rich.	ca. 36	VENEZUELA. GUÁRICO: 10 km NWN of Altagracia de Orituco, *Davidse 4187.*
Sacciolepis		
myuros (Lam.) Chase	18	VENEZUELA. BOLÍVAR: 27 km SW of Caicara, *Davidse 4353.*
Urochloa		
reptans (L.) Stapf	7	COSTA RICA. GUANACASTE: Hacienda Paloverde, *Pohl & Selva 12942.*

* First count for a species.
** Count differing from all previously reported ones for a species.

somes seemed more sharply contracted and stained less deeply than the normal bivalents. When two were present in a cell, they failed to pair, although they often were in close proximity. Meiosis was normal in other respects.

We have already reported $n = 30$ for two Venezuelan collections of *Pappophorum pappiferum* (Davidse & Pohl, 1974). Two other Venezuelan collections have $n = 50$ (Fig. 15). This species complex obviously is a derived polyploid complex with perplexing morphological variability. It seems probable that the different ploidy levels can be correlated with morphological differences. On the basis of morphology, the Venezuelan decaploids appear closely related to the decaploid populations of *P. bicolor* Fourn. known from Mexico and the southwestern United States (Gould, 1958, 1966; Reeder, 1968). Detailed cytotaxonomic studies may further elucidate the origin and relationships of these polyploids.

SUBFAMILY PANICOIDEAE

Chromosome numbers for three small American genera have been reported only in the last few years, but base numbers have not been established unequivocally because various investigators have reported different numbers for different species of the same genus or for the same species. Our two additional counts of $n = 10$ for *Echinolaena gracilis* from Venezuela and Colombia confirm one of our earlier counts for this species from Venezuela (Davidse & Pohl, 1974), but differ from the $2n = 18$ that we reported for a Costa Rican collection (Pohl & Davidse, 1971). Taking into consideration the count of $2n = 60$ reported for

FIGURES 1–13. First meiotic division in microsporocytes. Scale line equals 10 mμ.—1. *Chusquea scabra*, $n = 20$, diakinesis.—2. *Olyra lateralis*, $n = 18$, anaphase.—3. *Swallenochloa weberbaueri*, $n = 20$, diakinesis.—4. *Swallenochloa longiligulata*, $n = 20$, diakinesis.—5. *Agrostis turrialbae*, $n = 14$, anaphase.—6. *Calamagrostis intermedia*, diakinesis with

E. inflexa (Poir.) Chase by Gould & Soderstrom (1967), there now seems little doubt that $x = 10$ is the base number for this genus. The count of $n = 10$ for a Mexican collection of *Homolepis aturensis* agrees with an earlier count of $2n = 20$ for a Costa Rican collection (Pohl & Davidse, 1971), although Gould & Soderstrom (1970) reported $2n = 22$ from Colombia. Our counts, plus $2n = 40$ reported by Gould & Soderstrom (1967) for *H. isocalycia* (Meyer) Chase, definitely point to $x = 10$ as a base number. *Otachyrium versicolor* from Brazil was reported to have the approximate number $2n = 18$ by Gould & Soderstrom (1967). We obtained a definite count of $n = 10$ for this species. This, along with the earlier count of $n = 10$ for *O. inaequale* (Pilger) Pilger (Davidse & Pohl, 1974), firmly establishes the base number $x = 10$ for the genus.

Although we could not reconfirm the exact count of $n = 20$ for *Ichnanthus nemorosus* (Tateoka, 1962; Reeder, 1967; Pohl & Davidse, 1971; Davidse & Pohl, 1972a, 1972b), we could confirm the probable tetraploid nature of our current collection. We also noted the consistent presence of lagging univalents at anaphase I. Because of limited material, no further study of these irregularities could be made. Recent students of the genus *Ichnanthus* differ widely in their estimates of the number of species. The plants display perplexing morphological variability in the field and great cytological complexity as well. The genus is in definite need of further biosystematic study.

No unanimity exists as to the chromosome numbers of two species of *Ischaemum*, *I. indicum*, and *I. rugosum*. Counts given for *I. indicum* (including *I. ciliare*) indicate base numbers of $x = 9$ and $x = 10$ and also show the existence of diploids, tetraploids, and hexaploids based on these numbers. Individual counts were reported as $n = 9$ from Costa Rica (Pohl & Davidse, 1971); $n = 18$ from Taiwan (Chen & Hsu, 1962) and from Sri Lanka (Gould & Soderstrom, 1974); $n = 27$ from Costa Rica (Celarier, 1957). Counts of $n = 10$ were from Costa Rica (present paper), Indonesia (Reeder & Soderstrom, 1968), India (Oke, 1971). A tetraploid with $n = 20$ was reported from India (Sindhe & Narayan, 1976). An aneuploid count of $n = 26$ was reported by Mehra & Sood (1974) from India. Obviously, a definitive study of this species is yet to be made, and this should include an analysis of reproductive methods to determine whether apomixis is involved.

Our current count for *I. rugosum* indicates $n = 9$, and three previous reports based upon four New World and one Indian accessions agree with this number (Celarier, 1957; Pohl & Davidse, 1971; Davidse & Pohl, 1974). Counts based on other Indian accessions have differed. Oke (1971) reported $n = 10, 20, 30$ for three different collections, Singh & Godward (1960) reported $2n = 20$ for one collection, and Sindhe & Narayan (1976) reported $2n = 44$ for one collection. In our material, we noted two chromosomes that consistently paired very loosely

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$5_{IV} + 18_{II}$.—7. *Festuca chiriquensis*, $n = 14$, diakinesis.—8. *Stipa hans-meyeri*, $n = 11$, diakinesis.—9. *Aristida riparia*, $n = 11$, diakinesis.—10. *Aristida setifolia*, $n = 11$, diakinesis.—11. *Aristida torta*, $n = 11$, diakinesis.—12. *Aristida venesuelae*, $n = 22$, diakinesis.—13. *Gymnopogon spicatus*, $n = 10$, diakinesis.

Figures 14–30. First meiotic division in microsporocytes. Scale line equals 10 mμ.—14. *Muhlenbergia lehmanniana*, $n = 10 + 2B$, diakinesis.—15. *Pappophorum pappiferum*, $n = 50$, diakinesis.—16. *Pereilema brasiliensis*, $n = 20$, metaphase.—17. *Andropogon hypogynous*, $n = 30$, diakinesis.—18. *Axonopus fissifolius*, $n = 30$, diakinesis.—19. *Axonopus pruinosis*,

in diakinesis (Fig. 20), and the interpretation of such figures may account for some of the reported differences.

Panicum macranthum, previously unknown cytologically, is a hexaploid ($n = 27$) with irregular meiosis. Very loose pairing was characteristic of diakinesis in our fixation. In all cells examined, one or two quadrivalents and/or hexavalents were observed. Bridges were commonly observed at anaphase I (Fig. 22), and excluded chromosomes and/or fragments were commonly observed at the later stages of both meiotic divisions. *Panicum parvifolium*, known as a diploid ($2n = 18$) from Madagascar (Tateoka, 1965) and as a tetraploid ($2n = 36$) from Costa Rica (Pohl & Davidse, 1971), is tetraploid in Colombia. In our Colombian material, 9 large and 9 small bivalents were observed. Viewed only at metaphase I, the small bivalents could easily have been interpreted as univalents inasmuch as they had a tendency to align themselves tardily on the metaphase plate (Fig. 24). However, both anaphase I and anaphase II were normal, 18 chromosomes segregating to each pole. Furthermore, all pollen seemed fully formed, further negating the possibility of a $9_{II} + 9_{I}$ interpretation.

Paspalum carinatum, a characteristic species of South American savannas was previously known as a tetraploid, $n = 20$, at the periphery of its distribution in Nicaragua (Davidse & Pohl, 1972b). The present determination of a Venezuelan collection is diploid, $n = 10$, with regular meiosis (Fig. 26). Our first count for *Paspalum gardnerianum* shows it to be a tetraploid with $n =$ ca. 20 (Fig. 27). The sticky chromosomes of the material made it difficult to interpret the chromosome associations; hence, our count is tentative. Some cells, however, clearly showed up to three quadrivalents. Our Costa Rican collection of *Paspalum minus*, $n = 25$, also had meiotic irregularities. Although the majority of the chromosomes seemed at least loosely paired in diakinesis, we never observed more than 5 bivalents (Fig. 28) and sometimes as few as two in metaphase I. This is the first report of a pentaploid in this species, although diploids (Banks, 1966), tetraploids (Gould, 1958), and hexaploids (Moraes Fernandes et al., 1974) have been reported. It is likely that our collection is of hybrid origin and that the meiotic irregularities, not reported before in this species nor in our tetraploid collection from Colombia, can be traced to this origin. In *Paspalum notatum* from Costa Rica, we observed one or two quadrivalents in all the numerous cells examined (Fig. 29). Such multivalent associations in the tetraploid race of the species also have been noted by Forbes & Burton (1961) and Moraes Fernandes et al. (1974).

We found *Pennisetum setosum* to be octoploid with irregular meiosis, $n =$ ca.

←

$n = 30$, diakinesis.—20. *Ischaemum rugosum*, $n = 9$, diakinesis, arrow indicates loosely paired chromosomes.—21. *Panicum guianense*, $n = 20$, metaphase.—22. *Panicum macranthum*, $n = 27$, anaphase with one bride.—23. *Panicum olyroides*, $n = 18$, diakinesis.—24. *Panicum parviflorum*, $n = 18$, metaphase with 9 large and 9 small bivalents.—25. *Panicum pyrularium*, $n = 18$, diakinesis.—26. *Paspalum carinatum*, $n = 10$, metaphase.—27. *Paspalum gardnerianum*, $n =$ ca. 20, diakinesis with 1 quadrivalent.—28. *Paspalum minus*, metaphase with $5_{II} + 40_{I}$.—29. *Paspalum notatum*, diakinesis with $2_{IV} + 16_{II}$.—30. *Pennisetum setosum*, $n = 18$, diakinesis with 1 unusually large bivalent.

36, in one Venezuelan collection and tetraploid with regular meiosis, $n = 18$, in a Colombian collection. The latter is the lowest ploidy level known for this species. This tetraploid also had an unusually large chromosome pair, very similar in size to a quadrivalent (Fig. 30). Previous records for this species have been $2n = 53$ with irregular meiosis (Pohl & Davidse, 1971), $2n = 54$ (Avdulov, 1928), $n = 36$ with irregular meiosis (Davidse & Pohl, 1972a), and $2n = 78$ with irregular meiosis (Gould, 1965). As we have noted earlier, the irregular meiosis and different ploidy levels probably are the result of an apomictic breeding system (Pohl & Davidse, 1971).

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A CONTRIBUTION TO CYTOLOGY IN CORNALES[1]

PETER GOLDBLATT[2]

ABSTRACT

Chromosome counts in *Nyssa* and *Camptotheca* indicate a base number of $x = 22$ for Nyssaceae. *Davidia*, the only genus of Davidiaceae, has $x = 21$. In Cornaceae, where $x = 11$ was thought basic, *Mastixia* has $n = 13$ and 11, while *Curtisia*, recently excluded from Cornaceae as Curtisiaceae, has $n = 13$. Nyssaceae and Davidiaceae appear more closely related to Cornaceae than previously recognized subfamilies and tribes of this family, and segregation of *Helwingia*, *Mastixia* and *Curtisia* from Cornaceae as proposed by other workers is supported on cytological grounds.

While preparing a review of angiosperm cytology in relation to phylogeny, Raven (1975) was able to point out important gaps in the chromosome record for flowering plants. One of the groups where information was conspicuously lacking was the Cornaceae and its allied families Nyssaceae, Davidiaceae, and segregates such as Curtisiaceae.

An attempt was made to learn more of the cytology of these families, and by the time the review went to press (Raven, 1975), chromosome numbers had been determined for several rare and taxonomically critical genera. Most of these counts were available in time for inclusion in the review, but were not fully documented there. This paper, therefore, presents in detail the results of this recent chromosomal study with a short discussion of the possible significance to the systematics of the families concerned. The counts were made mainly by the writer but also by L. Rüdenberg and W. Tai, and with their permission, are also reported here.

MATERIALS, METHODS, AND OBSERVATIONS

Meiotic studies were made of most of the species investigated. Buds were fixed in Carnoy's solution (ethanol-acetic acid, 3:1) and stored in 70% ethanol.

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[1] Thanks are extended to the following for their assistance in providing materials used in this study: D. E. Breedlove, California Academy of Sciences, for buds of *Davidia involucrata* from plants at the Strybing Arboretum; Setijati Sastrapadja, Director, National Biological Institute, Bogor, Indonesia, for buds of *Mastixia trichotoma*; K. M. Matthew, St. Joseph's College, Tiruchirapalli, India, for buds of *M. arborea*; B. Bartholomew, University of California Botanic Garden, for seeds of *Cornus capitata*; and R. H. Eyde, Smithsonian Institution, for *Nyssa sylvatica* var. *sylvatica* and for arranging the collection of buds of *N. ogeche* by R. K. Godfrey, Florida State University, and *N. sylvatica* var. *biflora* by J. Stubbs, U.S. Forest Service.

Counts for *Mastixia trichotoma* were made by W. Tai, Department of Botany and Plant Pathology, Michigan State University, while Lily Rüdenberg, Gray Herbarium, Harvard University, counted one of the collections of *Davidia involucrata* studied here.

The author is recipient of grant DEB-76-19907 from the U.S. National Science Foundation. Collection of *Mastixia arborea* was made possible by a travel grant to Dr. Eyde from the Smithsonian Institution's Foreign Currency Program.

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ANN. MISSOURI BOT. GARD. 65: 650–655. 1978.

0026-6493/78/0650–0655/$00.75/0

Mitotic studies were made in the case of *Mastixia trichotoma*, where a count was obtained from tapetal cells of developing anthers, and from root tips in *Camptotheca*, *Cornus capitata* and *Curtisia*. *Camptotheca* cuttings were supplied by the U.S. Department of Agriculture Plant Introduction Station, Chico, California, and grown at the Missouri Botanical Garden. *Curtisia* and *Cornus capitata* were grown from seed collected in the wild and also grown at the Missouri Botanical Garden. Root tips were pretreated in 0.003 M hydroxyquinoline for five hours at refrigerator temperature. After fixation they were hydrolyzed in 10% HCl and stained in lactopropionic orcein (Goldblatt, 1976). Chromosome counts obtained in the study are listed in Table 1, where collection data and voucher information is also given.

Discussion

At the time that this study was undertaken, the chromosome number was already well known in *Nyssa* with reports of $n = 22$ in *N. javanica* (Mehra & Bawa, 1969; Mehra, 1972) and in *N. sylvatica* (Dermen, 1932; Eyde, 1963; $n = 22 \pm 1$ being reported). The present study confirms $n = 22$ as fundamental in this genus, with reports for *N. ogeche* and *N. sylvatica* var. *biflora* representing first counts for these taxa.

In the other genus of Nyssaceae, the closely related *Camptotheca*, Raven (in Perdue, 1970) reported $n = 21$. Reexamining the same material of *C. acuminata* I find $n =$ ca. 22. Both records for *Camptotheca* were mitotic and in view of the numerous and small chromosomes in this species a meiotic count would be valuable in finally establishing its chromosome number.

In the monotypic *Davidia*, sometimes treated as a separate family, as here, following several recent authors (e.g., Cronquist, 1968), but otherwise placed in Nyssaceae, Dermen (1932) reported $n =$ ca. 20. The number for this close relative of Nyssaceae is now firmly established as $n = 21$ from two different sources, one count made by L. Rüdenberg and the other one by myself. This difference in chromosome number would support the belief that *Davidia* may be phylogenetically somewhat removed from *Nyssa* and *Camptotheca*, the two genera with which it is most often allied. The difference does not in itself necessarily imply familial separation, and the general relationship of *Davidia* to *Nyssa* and *Camptotheca* is not questioned. Fairbrothers (1977), on the basis of serological evidence also supports the separation of *Davidia* from *Nyssa* and *Camptotheca* and suggests subfamilial status for the two groups.

Cornaceae is a more heterogeneous family. As treated by Melchior (1964), following the classical treatment of Wangerin (1910), it was divided into three subfamilies, Curtisioideae, Mastixioideae, and Cornoideae, the latter with tribes Toricellieae, Helwingieae, Corneae, and Griselinieae. Treated here with Curtisioideae recognized as a separate family (Eyde, 1967; Takhtajan, 1970; Airy Shaw, 1972), Cornaceae remains the largest family in the cornalean alliance. A base number of $x = 11$ is well established for tribe Corneae, which also has $n = 10$, 9 in *Cornus* itself, with $n = 8$ in *Aucuba* and $n = 9$ in *Corokia*, both genera probably not correctly placed in Corneae (Adams, 1949) or even

TABLE 1. Chromosome counts for Cornaceae, Nyssaceae, Davidiaceae and Curtisiaceae obtained in this study. Voucher and collection information is presented as far as it is known.

Species	Chromosome No. *n*	Chromosome No. 2*n*	Collection and Voucher
	NYSSACEAE		
Nyssa sylvatica Marsh. var. *sylvatica*	22		Cultivated at U.S. National Arboretum (native of U.S.A.), *Eyde 120* (US).
N. sylvatica var. *biflora* (Walt.) Sargent	22		U.S.A., South Carolina, Berkeley Co., Santee swamp, *Priester s.n.* (MO).
N. ogeche Bartr. ex Marsh.	22		U.S.A., Florida, Liberty Co., *Godfrey 74223* (US).
Camptotheca acuminata Dec.		ca. 44	China, Chang An, Yung, Hsian (cult. U.S. Dept. Agriculture Plant Introduction Stn., Chico, California) (NA).
	DAVIDIACEAE		
Davidia involucrata Baill. var. *vilmoriniana* (Dode) Wangerin	21[a]		Cultivated at Arnold Arboretum, seed originally collected in Szech'uan, China, *Rehder s.n.* (AA).
	21		Cultivated at Strybing Arboretum, San Francisco, California, (CA).
	CORNACEAE—Mastixioideae		
Mastixia trichotoma Blume		22[b]	Indonesia, cult. at Cibodas Mountain Gardens, Bogor, (representative material at BO).
M. arborea (Wight) C. B. Cl.	13		India, Mysore State, Agumbe State Forest, Shimoge distr. *Matthew 14472* (US).
	CORNACEAE—Cornoideae		
Cornus capitata Wall.		22	Bhutan, E of Sintoka Dzong, *Bartholomew 209* (BM, UC).
	CURTISIACEAE		
Curtisia dentata (Burm. f.) C. A. Sm.		26	South Africa, Cape, Contour Path, Kirstenbosch, *Compton 8092* (NBG).

[a] Chromosome count made by Lily Rüdenberg, Gray Herbarium, Harvard University.
[b] Chromosome count made by W. Tai, Michigan State University.

Cornaceae (Eyde, 1964, 1967; Fairbrothers, 1977). The count of $n = 11$ reported here for *Cornus capitata* in fact confirms an earlier record for the species and clearly is representative of this tribe.

In the other tribes of Cornoideae, Griselinieae has as far as is known $x = 9$ ($n = 18$ in *Griselinia*, Federov, 1969; Raven, 1975) and Helwingeae $x = 19$ (Hara & Kurosawa, 1975). Helwingeae may in fact not be related at all to Cornaceae (see below). The remaining tribe, Toricellieae has $2n = 24$ (Malla et al., 1978), this based on a report for one of the three species of *Toricellia*, the only genus of the tribe. The count suggests that *Toricellia* might not be related to Cornaceae and the alternative placement in Araliaceae which has $x = 12$ (Raven, 1975) may be correct.

Counts here for *Mastixia*, the sole genus of Mastixioideae, are the first records for this subfamily. The situation in *Mastixia* with $n = 13$ and $n = 11$ in separate species is unclear as yet and appears complex. This range of chromosome number is unexpected in a genus of tropical, woody plants and requires confirmation. However, on present evidence $x = 13$ may be basic for Mastixioideae, which appears to support the placement of *Mastixia* in a separate subfamily of Cornaceae.

The monotypic African Curtisiaceae has a base number of $x = 13$, with $2n = 26$ in *Curtisia dentata*. If Curtisiaceae is, as generally accepted, fairly primitive in the cornalean alliance, the view that $x = 11$ is basic and fundamental in Cornales must be questioned. It seems that $x = 13$ or 14 may be ancestral with early reduction to 11 in Cornaceae and closely related families as Raven (1975: 740) postulated. The record of both $n = 13$ and 11 in Mastixioideae, though requiring further study, suggests a link between Curtisiaceae and Cornaceae.

With *Curtisia* and perhaps *Mastixia* excluded, $x = 11$ seems basic in Cornaceae. Evolution within Cornaceae appears to have involved aneuploid reduction, giving rise to $n = 10$ and 9 in Corneae and $x = 9$ in Griselinieae, assuming its position in Cornaceae is correct. *Helwingia*, with $n = 19$ firmly established, is problematic and its placement in Cornaceae has been seriously questioned by several systematists. Eyde (1966: 845; 1967: 177) supports its removal from Cornaceae on the basis of carpel vasculature not corresponding to the peculiar pattern in *Cornus* and its allies. Hutchinson (1967: 74) assigns *Helwingia* to Araliaceae where, however, its chromosome number conflicts sharply with $x = 12$ in all members of this family known cytologically. It is of interest to point out that *Helwingia*, of all Cornaceae and allied families, lacks the taxonomically significant iridoid compounds (Bate-Smith et al., 1975) and thus from a chemical point of view also seems best excluded from any cornalean alliance.

The two monogeneric families, Garryaceae and Alangiaceae, generally believed to be closely related to Cornaceae are known to have $x = 11$. The cytology certainly supports this view but does not exclude alternatives (Eyde, 1968, 1972).

Chromosome numbers appear to indicate a close relationship between Cornaceae-Cornoideae, Nyssaceae and Davidiaceae, with $x = 22$ in Nyssaceae possibly related by direct polyploidy to the $x = 11$, basic in Cornoideae. In fact, at least from a cytological point of view, Nyssaceae (and Davidiaceae) seem to be more closely related to Cornaceae than is Curtisiaceae. Recognition of this

family thus seems indicated on cytological as well as morphological and anatomical grounds. *Curtisia* also lacks the unusual carpel vasculature of Cornaceae, Nyssaceae, and Davidiaceae (Eyde, 1967).

There are still gaps in our knowledge of the cytology of Cornales and, in view of the information presented here, counts are most desirable for the two Madagascan genera, *Kaliphora* and *Melanophylla*, both of unknown affinities, though assigned by Wangerin (1910) to Cornaceae—Corneae and —Griselinieae, respectively. Cytological data on these two genera would be particularly valuable since both were excluded with *Curtisia* from Cornaceae by Eyde (1967) on anatomical grounds. *Melanophylla* has recently been placed in its own family (Takhtajan, 1970; Airy Shaw, 1972), while *Kaliphora* has been associated with the Afro-Madagascan Montiniaceae (Capuron, 1969; Krach, 1976; Dahlgren et al., 1977).

In summary, chromosome cytology can be said to suggest the following:

1. Nyssaceae, $n = 22$, and Davidiaceae, $n = 21$, stand out as being fundamentally hexaploid in the cornalean alliance and may be related by direct polyploidy to Cornaceae—Cornoideae, in which $x = 11$ is basic.

2. Cornaceae—Cornoideae—Corneae with $x = 11$ (and secondary aneuploidy) seem more closely related to the specialized Garryaceae and Alangiaceae (both also $x = 11$) than to Cornoideae—Griselinieae, —Toricellieae and —Helwingeae as well as to the traditionally recognized subfamilies of Cornaceae, Curtisioideae, and Mastixioideae.

3. Cytology provides support for the exclusion of *Curtisia* from Cornaceae based on other lines of evidence, while bringing into question the relationship of *Mastixia* and *Toricellia* to Cornaceae.

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REPRODUCTIVE STRUCTURES AND EVOLUTION IN *LUDWIGIA* (ONAGRACEAE). II. FRUIT AND SEED[1]

Richard H. Eyde[2]

Abstract

Ludwigia seed coats cut in various ways and examined with light microscope and with SEM have four similar cell layers regardless of species, noteworthy modifications occurring only in taxa with seeds fused to the fruit wall. Surface features of the seeds are also much alike except in *Microcarpium*, a diverse section in which some of the species deviate with respect to the orientation of epidermal cells. In sections *Ludwigia*, *Macrocarpon*, and *Myrtocarpus*, but not in sections *Dantia* and *Microcarpium*, the fruit wall has a well-differentiated inner zone of spongy tissue that reduces the wall's effective thickness when dry, thereby aiding seed dispersal. In section *Seminuda* and three monotypic sections similar tissue, spongy at early stages, increases and changes into a buoyant, protective endocarp as the fruit grows. In section *Oligospermum* and in *L. torulosa* endocarps form without an initial spongy stage; they differ from *Seminuda* endocarps in that the inner epidermis becomes a zone of woody fibers several cells thick. *Oligospermum* also stands apart because tissue surrounding the endocarp is aerenchymatous; this section therefore seems to have diverged early from the other ludwigias and developed its own aquatic adaptations. Evolutionary lengthening and narrowing of the inferior ovary has taken place repeatedly in *Ludwigia*, accompanied by reduction in the number of ovules per cross-section. Evolution of protective endocarp followed wherever reduction progressed to the 1-seriate condition, bringing developing seeds into intimate contact with the fruit wall.

Keys for identifying the species of *Ludwigia* usually begin with stamen number, a legacy from Linnaeus. Distinguishing features of greater evolutionary importance, however, are the uniseriate or pluriseriate arrangement of ovules and the presence or absence of persistent endocarp tissue around mature seeds. Illustrations of uniseriate and pluriseriate ovules accompanying the section on placentation in an earlier article (Eyde, 1977); I continue here with the anatomy of the seed coats and the fruit.

Corner's (1976) observations and illustrations of *Ludwigia* ("*Jussieua*") *peruviana* have aided me; not so the earlier literature. Ohlendorf (1907) could see only one cell layer in a tegmen that is really 2-layered. Rode (1913) saw one layer too many in the testa. Van Wisselingh's (1920) description and sketch, which reappeared in Netolitzky's (1926) compilation, are accurate, but brief; moreover, one cannot tell what ludwigia van Wisselingh or Rode worked with. Rode's "spindelformig" seeds were supposed to be those of *Jussieua angustifolia*. This name is a synonym of *L. octovalvis*, however, and the seeds of *L. octovalvis* are not spindle shaped. Van Wisselingh identified his material as *L. mullertii* hort., a name now applied to a seedless plant (Mühlberg, 1972).

My observations are taken from vouchered material prepared in a number

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[1] I thank D. Dille, T. P. Ramamoorthy, and P. Raven for criticizing the typescript. The National Science Foundation contributed indirectly, via a series of grants to Raven, by supporting the field work of several collectors. Photographs and anatomical preparations are the work of Smithsonian photographer V. Krantz and museum specialist S. Yankowski, respectively.

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Ann. Missouri Bot. Gard. 65: 656–675. 1978.

0026-6493/78/0656–0675/$02.15/0

of ways. For developmental stages, I used stained serial sections of paraffin-imbedded specimens. Fully hardened seeds were affixed singly to a Komatsu Electro Freeze freezing stage, sectioned freehand under a dissecting microscope with a single-edge razor blade, and stained with toluidine blue O, a method devised by S. Yankowski. I obtained clean endocarps by boiling herbarium fruits in diluted NaOH (5 g/100 ml H_2O) then in H_2O alone, repeating until the outer pulp came free. I also examined endocarp tissue that had been treated with a 1/1 mixture of 10% nitric acid and 10% chromic acid to separate the cells, and I used a scanning electron microscope for 3-dimensional visualization of seeds and endocarps.

Herbarium vouchers for most of the sectioned material are tabulated in my previous article. Though the table's caption says "sectioned *Ludwigia* flowers," many of the collections included fruits in various stages of development. Vouchers for seeds scanned electronically are listed in Table 1 of the present article. Dimensions of fruits and seeds are taken from regional treatments (Munz, 1942, 1965, 1974; Raven, 1963, 1977).

Section *Myrtocarpus*

In this group of about 40 species (Ramamoorthy, unpubl.), the size of the mostly obconic or obpyramidal capsules differs substantially from one species to another, capsules of *Ludwigia decurrens* or *L. erecta* being as short as 12 mm, those of *L. longifolia* as long as 35 mm. The capsule wall is made up of a single inner epidermal layer of transversely elongate cells, a single outer epidermal layer, and an intervening parenchyma a few cells thick to more than 15 cells thick, depending on the species and the developmental stage of the capsule. Paired raphide idioblasts, widely distributed in vegetative parts of Onagraceae (Metcalfe & Chalk, 1950; Carlquist, 1975), develop in the parenchyma of all *Ludwigia* fruits.

The inner parenchyma layers of the ovary become spongy in five of the seven *Myrtocarpus* species I have examined: *Ludwigia decurrens*, *L. erecta*, *L. foliobracteolata*, *L. peruviana*, and *L. tomentosa*. The cells separate from their neighbors at least to the extent that conspicuous air spaces form and cell outlines become irregular (Fig. 1). In cross-section or longitudinal section the tissue then resembles the spongy parenchyma of a leaf or a petal or the separation tissue in developing fruits of the melastomataceous genus *Rhexia* (Eyde & Teeri, 1967). As in *Rhexia*, some postfertilization cross-sections show a complete separation of the outer parenchyma from a narrow zone of cells—epidermis and adhering spongy parenchyma—surrounding the locules (Fig. 2). The two *Myrtocarpus* species in which I have found spongy parenchyma poorly developed or lacking (Fig. 3) are exceptional members of the section in other ways: *Ludwigia densiflora* has very tough, almost cylindrical fruits and bears flowers in spikes; *L. latifolia* has pollen in isolated packets (Eyde, 1977).

Seeds of section *Myrtocarpus* can be as short as 0.3 mm (*Ludwigia decurrens*), as long as 1 mm (*L. mexiae*, *L. nervosa*). Usually obovoid (sometimes slightly curved), they are ¼ to ½ as wide as they are long. The raphe is commonly about

TABLE 1. Herbarium vouchers for *Ludwigia* seeds scanned with SEM. All are in the U.S. National Herbarium.

Taxa	Vouchers
Sect. *Cryptosperma*	
L. abyssinica A. Rich.	*Thomas III33* (US-554592), Kenya.
Sect. *Dantia*	
L. arcuata Walt.	*Godfrey & Reinert 61100*, Florida.
L. palustris (L.) Ell.	*Horner 618*, Washington.
L. spathulata Torr. & A. Gray	*Curtiss 6853*, Florida.
Sect. *Fissendocarpa*	
L. hyssopifolia (G. Don) Exell	*Ferreyra 1158*, Peru.
Sect. *Ludwigia*	
L. alternifolia L.	*Whitehouse 16350*, Texas.
L. hirtella Raf.	*Cory 56641*, Texas.
L. maritima Harper	*Pollard 1112*, Mississippi.
L. virgata Michx.	*Godfrey & Tryon 523*, South Carolina.
Sect. *Macrocarpon*	
L. lagunae (Morong) Hara	*Lorentz*, no number (US-1233717), Paraguay.
L. octovalvis (Jacq.) Raven	*Anderson 8336*, Brazil.
Sect. *Microcarpium*	
L. alata Ell.	*Fernald et al. 4960*, Virginia.
L. curtissii Chapman	*Godfrey 65514*, Florida.
L. glandulosa Walt.	*Smith 1938*, Alabama.
	Tracy 8496, Louisiana.
L. lanceolata Ell.	*Harper 1605*, Georgia.
L. linearis Walt.	*Vanderbilt 4175d*, South Carolina.
L. linifolia Poir.	*Godfrey 6195*, North Carolina.
L. microcarpa Michx.	*Godfrey & Reinert 60969*, Florida.
L. pilosa Walt.	*Cory 49815*, Texas.
	Trécul 915, Mississippi.
L. polycarpa Short & Peter	*Benke 4926*, Illinois.
	Bissell & Clark 245, Connecticut.
L. simpsonii Chapman	*Godfrey & Reinert 60970*, Florida.
L. sphaerocarpa Ell.	*Kral 44739*, Alabama.
L. suffruticosa Walt.	*Jones 79*, Florida.
Sect. *Miquelia*	
L. ovalis Miq.	Collector unknown (US-350866), Japan.
Sect. *Myrtocarpus*	
L. brachyphylla (Mich.) Hara	*Anderson 6297*, Brazil.
L. decurrens Walt.	*Prance et al. 5665*, Brazil.
L. densiflora (Mich.) Hara	*Macedo 3940*, Brazil.
	Rusby 1792, Brazil.
L. elegans (Camb.) Hara	*Campinas 446*, Brazil.
L. erecta (L.) Hara	*Prance et al. 10331*, Brazil.
L. latifolia (Benth.) Hara	*Gleason 676*, British Guiana.
	Klug 1738, Colombia.
L. lithospermifolia (Mich.) Hara	*Anderson 7866*, Brazil.
L. longifolia (DC.) Hara	*Bridorolli 3005*, Argentina.
L. nervosa (Poir.) Hara	*Killip 34404*, Colombia.
L. peruviana (L.) Hara	*Jorgensen 4122*, Paraguay.
	Killip & Smith 20497, Colombia.
L. sedoides (Humb. & Bonpl.) Hara	*Cuatrecasas 19654*, Colombia.

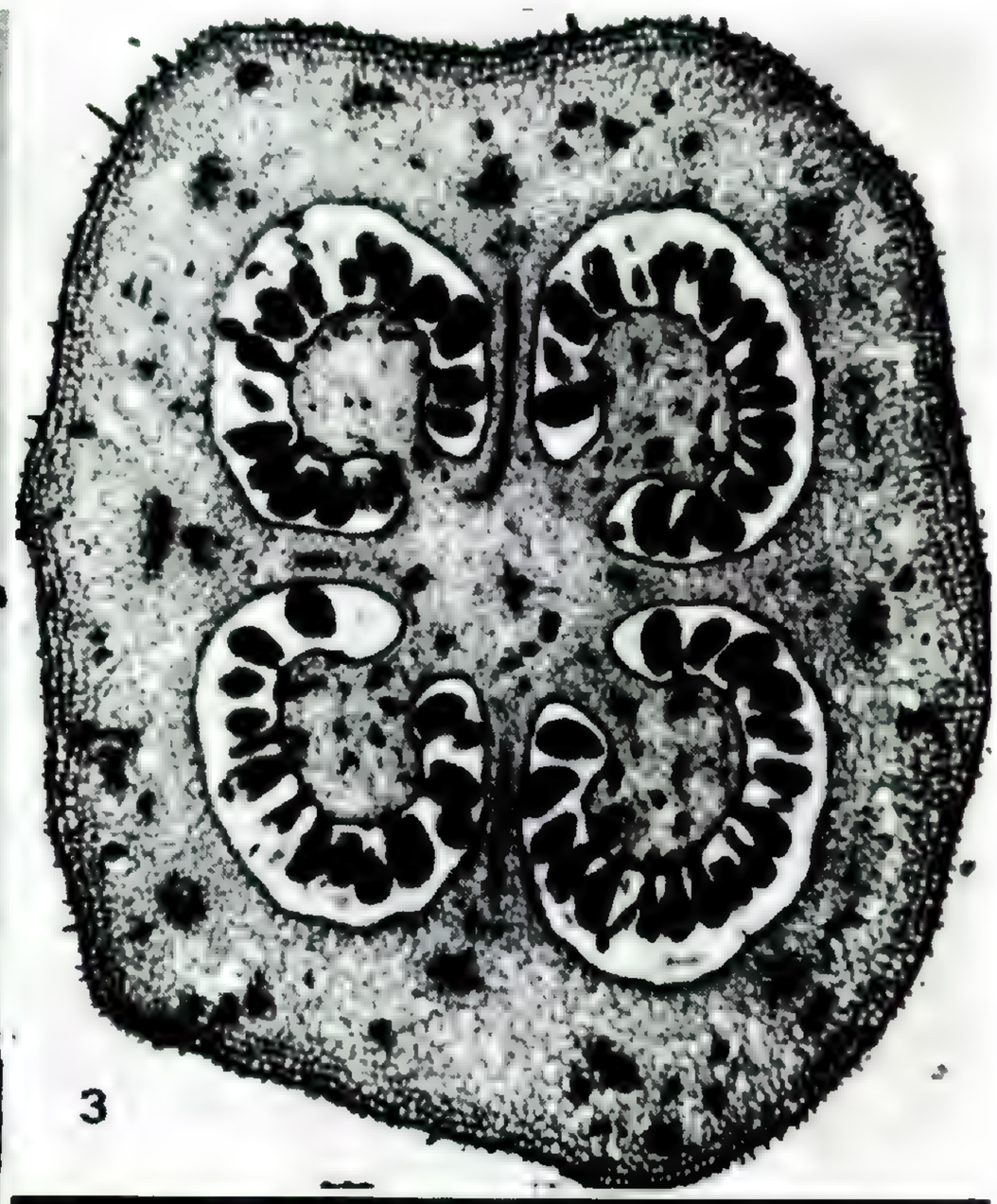
TABLE 1. (continued)

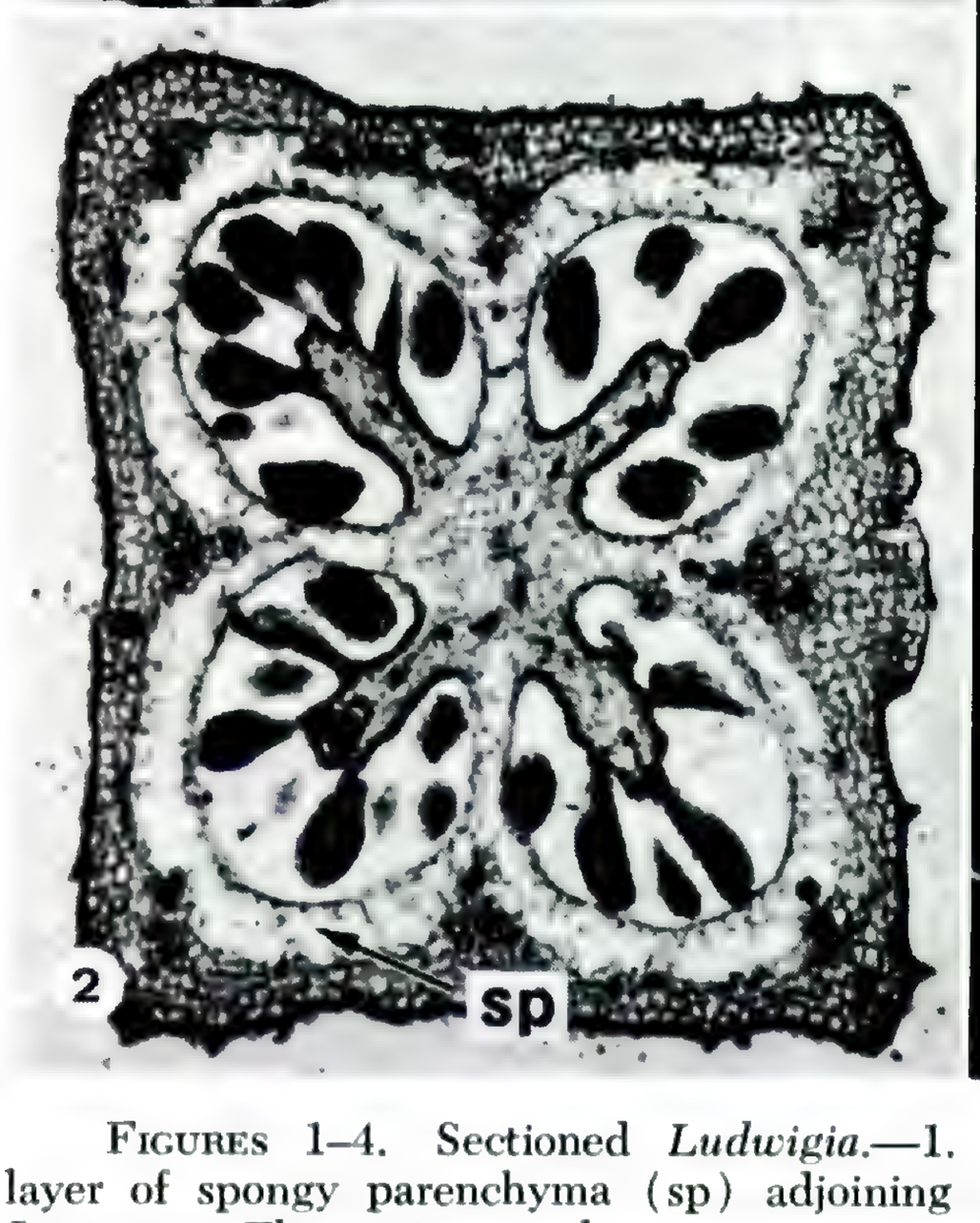
Taxa	Vouchers
Sect. *Nipponia*	
L. epilobioides Maxim.	*Tokyo Science Museum 1130*, Japan.
Sect. *Oligospermum*	
L. peploides (H.B.K.) Raven	*Ruth 716*, Texas.
Sect. *Oocarpon*	
L. torulosa (Arnott) Hara	*Cowan 38886*, French Guiana.
Sect. *Seminuda*	
L. leptocarpa (Nutt.) Hara	*Proctor 16898*, Grenada.

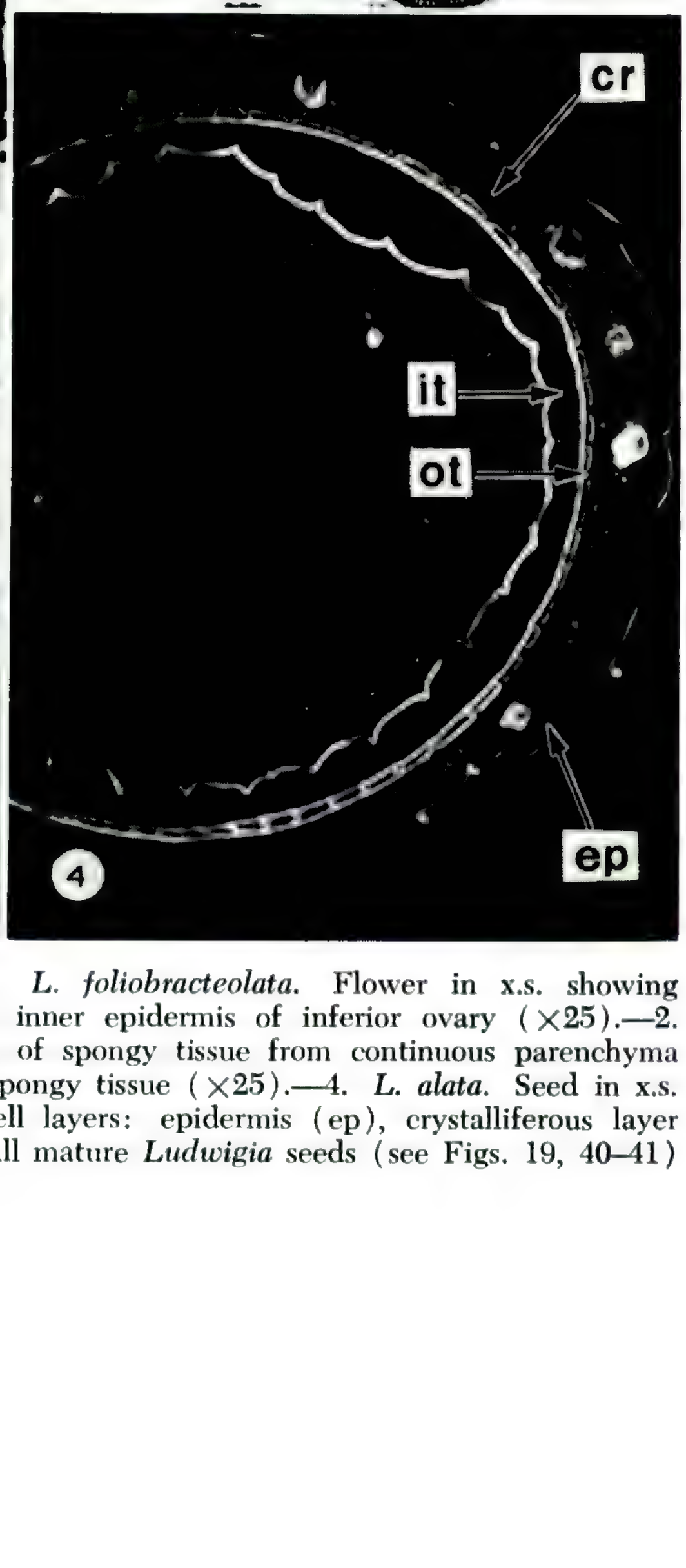
⅕ as wide as the body of the seed but can be ½ as wide in *L. foliobracteolata*. Corner's (1976) observations on the seed histology of *Ludwigia peruviana* are valid for other species of section *Myrtocarpus* and for most species outside the section (see Fig. 4). The testa has two cell layers: an outer layer of transversely elongate cells and an inner layer of crystalliferous cells. The inner and radial walls of the crystalliferous cells are lignified and very thick. The tegmen is also 2-layered, the outer cells being thick walled and longitudinally very elongate, the inner thin walled and not so elongate. The cells of the inner layer are filled with a darkly staining substance. This layer tears easily when sectioned, and fragments of the darkly stained cells then adhere to the nucellus. Corner omitted two features reported in earlier works: the outer epidermal cells develop median longitudinal thickenings (Ohlendorf, 1907; van Wisselingh, 1920) that may protrude as tiny tangential ridges on the surface of a dry seed (Figs. 22, 33), and the crystalliferous cells frequently contain large solitary crystals (Rode, 1913) in addition to the small crystals described by Corner. At least some of the large crystals have diamond-shaped outlines, a form not found among the crystals in onagraceous woods (Carlquist, 1975).

Surface features of *Myrtocarpus* seeds will be illustrated by T. P. Ramamoorthy in a subsequent article; so I shall not treat surface features here except to mention that *Ludwigia densiflora* and *L. latifolia* again are unusual. In *L. densiflora*, the cell outlines and orientation vary more than they do in most ludwigias (compare Figs. 21–22). The surface cells of *L. latifolia* have exceptionally large cross-sections (as seen in sliced material), but the walls are no thicker than they are in other species; consequently, the cells collapse in the vacuum chamber of the scanning electron microscope, giving the seed a peculiar wrinkled appearance (Fig. 23).

Although all the mature *Ludwigia* seeds I have looked into have two cell layers in the testa and two in the tegmen, I have seen what appears to be a third layer in inner integuments of *L. peruviana* ovules that were fixed prior to fertilization. Possibly this species loses a layer of cells during maturation of the seed coat, but I am not completely confident of the observation because most of my paraffin sections are cut at about 15 μm, too thick for unequivocal counting of layers of small cells.







FIGURES 1–4. Sectioned *Ludwigia*.—1. *L. foliobracteolata*. Flower in x.s. showing layer of spongy parenchyma (sp) adjoining inner epidermis of inferior ovary (×25).—2. *L. erecta*. Flower in x.s. showing separation of spongy tissue from continuous parenchyma (×50).—3. *L. latifolia*. Flower in x.s.; no spongy tissue (×25).—4. *L. alata*. Seed in x.s. Phase-contrast, dark-field. Labels indicate cell layers: epidermis (ep), crystalliferous layer (cr), outer and inner tegmic layers (ot,it). All mature *Ludwigia* seeds (see Figs. 19, 40–41) have this 4-layered structure (×260).

Section *Ludwigia*

Capsules are smaller (length 4–8 mm) than they are in most *Myrtocarpus* species, and all are somewhat cuboidal, hence the common name, seedbox, for *L. alternifolia*. My slides were prepared from fairly mature fruits of two of the four species, *Ludwigia maritima* and *L. virgata,* and younger material of these species plus a third, *L. alternifolia*. The parenchyma of the developing fruit wall is commonly 12–15 cells thick, and an outer zone of continuous parenchyma surrounds an inner zone of spongy parenchyma, as in section *Myrtocarpus*. From the physiological standpoint, it is interesting that the zonation of the ovary wall develops before fertilization (Fig. 9). While the fruit develops, the walls of two or three layers of cells beneath the outer epidermis thicken and become lignified; as a result, the mature capsule is harder than the usual *Myrtocarpus* capsule. The zonate structure of the fruit wall is readily demonstrated with dry material, for the two layers separate when the capsule is crushed. The capsules open (always?) by an apical pore formed when the style abscises and subjacent tissue deteriorates (Raven, 1963: fig. 11). Abscission is preceded by cell divisions in the abscission zone (Figs. 5–6), but the process differs from leaf abscission in that there is no protective layer of suberized cells below the abscission zone. Deterioration of the tissue between the abscission zone and the seeds is doubtless aided by the heavy concentration of raphide idioblasts in this region. Styles can abscise in a similar way in section *Myrtocarpus*, leaving an apical depression, if not an actual pore (Figs. 7–8).

Histologically, the seeds of section *Ludwigia* resemble those of section *Myrtocarpus*. External sculpture is unexceptional: the transversely elongate cells are in parallel columns over the body of the seed (Fig. 24).

Sections *Dantia* and *Microcarpium*

Fruits in these closely related sections are quite small. Maximum length rarely exceeds 10 mm and minimum length may be as little as 1 mm in *Ludwigia microcarpa*. I have sectioned flowers of six species from these two groups, but I have had access to pickled fruits from only one species in each: *L. palustris* in *Dantia*, *L. alata* in *Microcarpium*. In both sections, the ovary wall has fewer cell layers than the ovary wall of most *Myrtocarpus* species. *Ludwigia palustris* is the extreme; here the parenchyma opposite the locules is fewer than 10 cells thick, and these cells remain small during fruit development (Fig. 10) while the cells in the septal radii enlarge. The tissue in the placental radii is so thin at maturity that the seeds can be seen clearly through the wall of a wet fruit. Inspection of intact herbarium fruits from other members of section *Dantia* indicates that they are similarly constructed, but none are as papery-thin as those of *L. palustris*. Fruits of *L. alata* have wings or heavy ridges opposite the locules; consequently, the fruit wall is thickest in the placental radii, contrasting markedly with the fruit wall in *Dantia* species and in most other species of section *Microcarpium*.

Monographers have observed that fruits of certain *Microcarpium* species dehisce by means of flaps separating from the top of the fruit (Raven, 1963:

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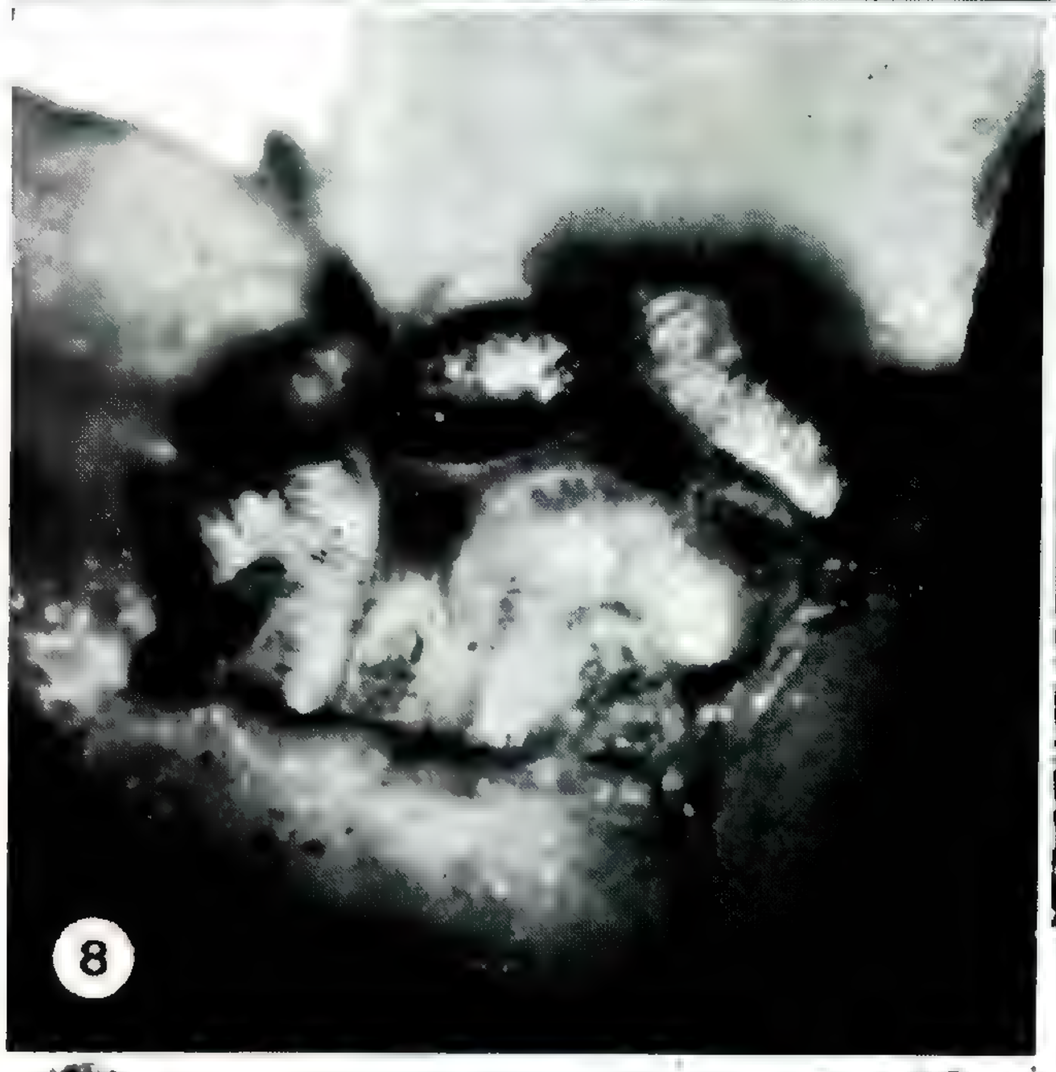
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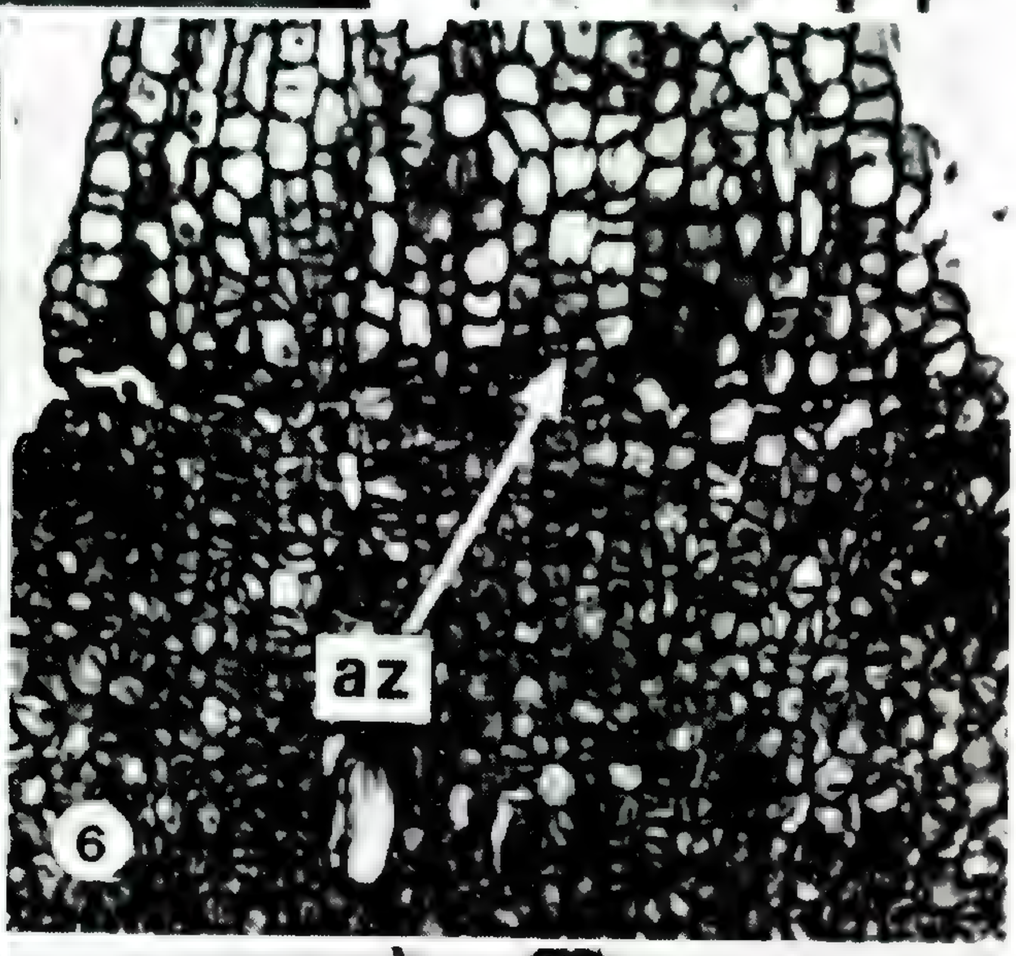

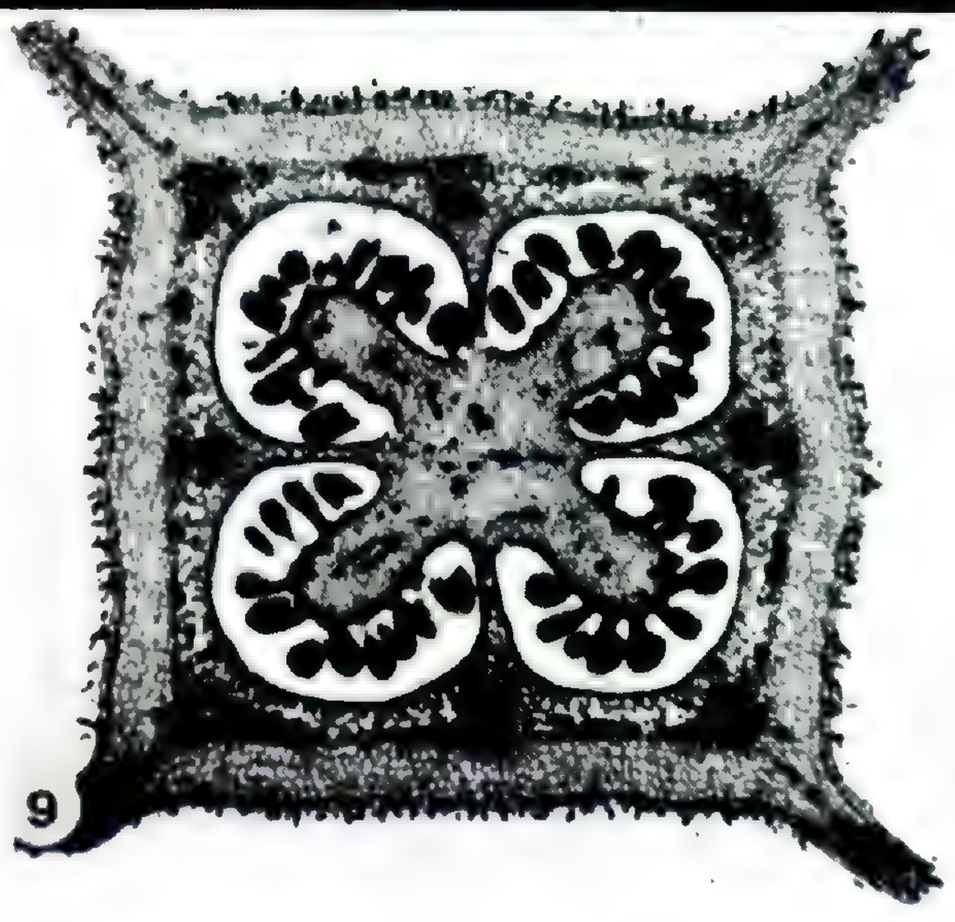
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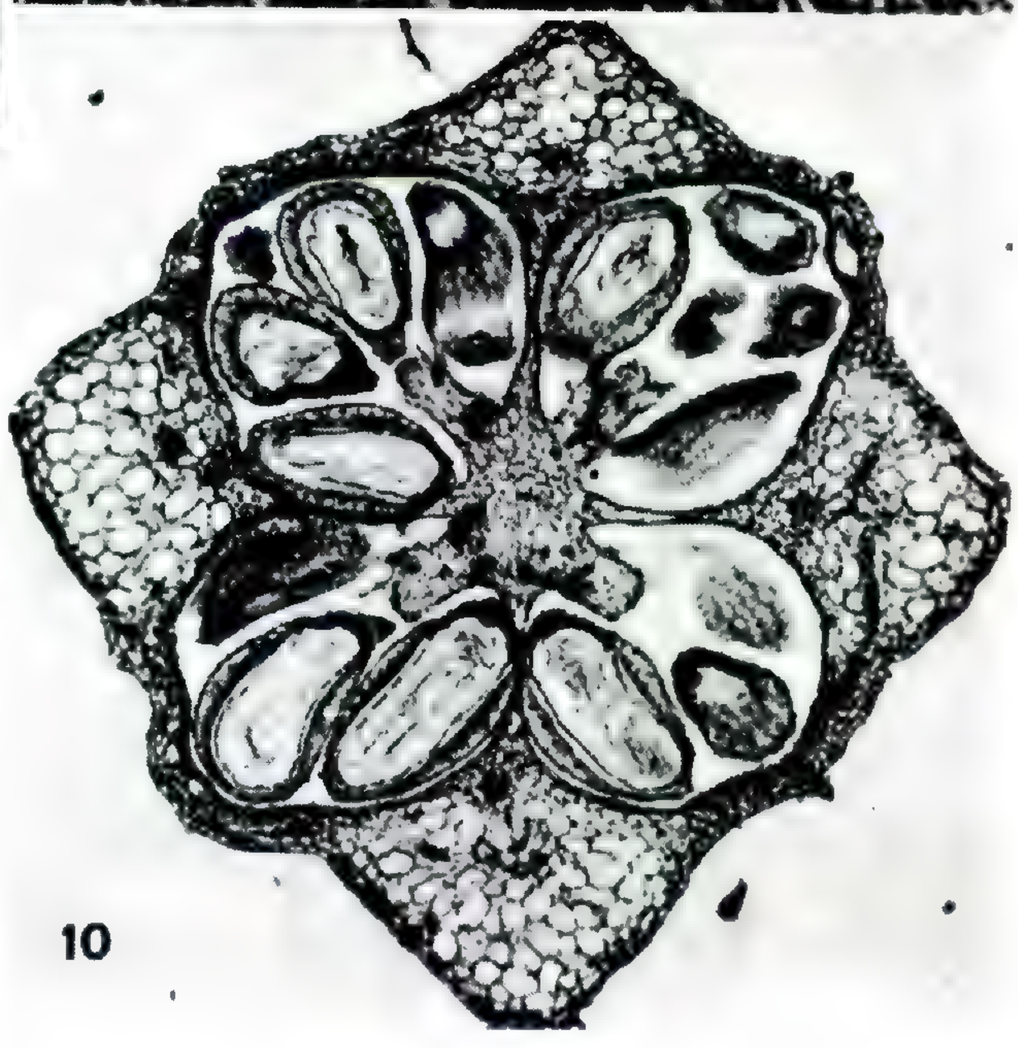
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fig. 12). Histological zonation of the fruit wall may have a role in this dehiscence, for I have seen some spongy parenchyma below the sepals in longitudinal sections of *Ludwigia pilosa* (the only spongy parenchyma I have observed in sections *Dantia* and *Microcarpium*). Histological zonation is also manifested in *L. pilosa*, but not in related species, by the abundance of dark-staining cells in the inner parenchyma layers of the ovary wall (Fig. 11).

In general, seeds of sections *Dantia* and *Microcarpium* are histologically similar to those of section *Myrtocarpus*, but in *Ludwigia palustris* the cells of the crystalliferous layer can differ greatly in size from one part of the seed to another, those in the middle of the seed being much larger than those at the ends.

The elongate surface cells of *Dantia* species have the usual transverse orientation (Fig. 25), but in section *Microcarpium* the surface features differ from species to species. *Ludwigia lanceolata*, *L. linifolia*, *L. pilosa*, and *L. suffruticosa* have more or less isodiametric surface cells (Fig. 26). In *L. polycarpa* and in a collection identified as *L. glandulosa*, the cells are elongate in the direction of the seed's length (Figs. 27–28). In a second collection identified as *L. glandulosa*, most surface cells are transversely elongate (Fig. 29), and they are transversely elongate in the remaining *Microcarpium* species that I examined (see Table 1).

Section *Macrocarpon*

The four closely related species have narrow cylindrical capsules up to 50 mm long. Eight prominent ribs mark the position of large vascular bundles in the locular and septal radii. I sectioned developing ovaries of *Ludwigia neograndiflora* and *L. octovalvis*, but the only mature *Macrocarpon* fruits I have seen were taken from pressed specimens. Parenchyma of the ovary wall is 10–15 cells thick. Effective thickness is less, however, because the inner parenchyma becomes lacunose early in development and tears away from the continuous outer parenchyma, thus presenting no barrier to rupture of intercostal areas when the fruit dies. Accordingly, fruits are more fragile and fall apart more easily than those of section *Myrtocarpus*.

Seeds of section *Macrocarpon* are unique in the genus in that the raphe grows to match the body of the seed in size and shape (Fig. 33). The appearance of seeds that have been cut transversely (Fig. 34) indicates that the parenchyma cells within the raphe do not divide but expand and then tear as the raphe's epidermal cells increase in number.

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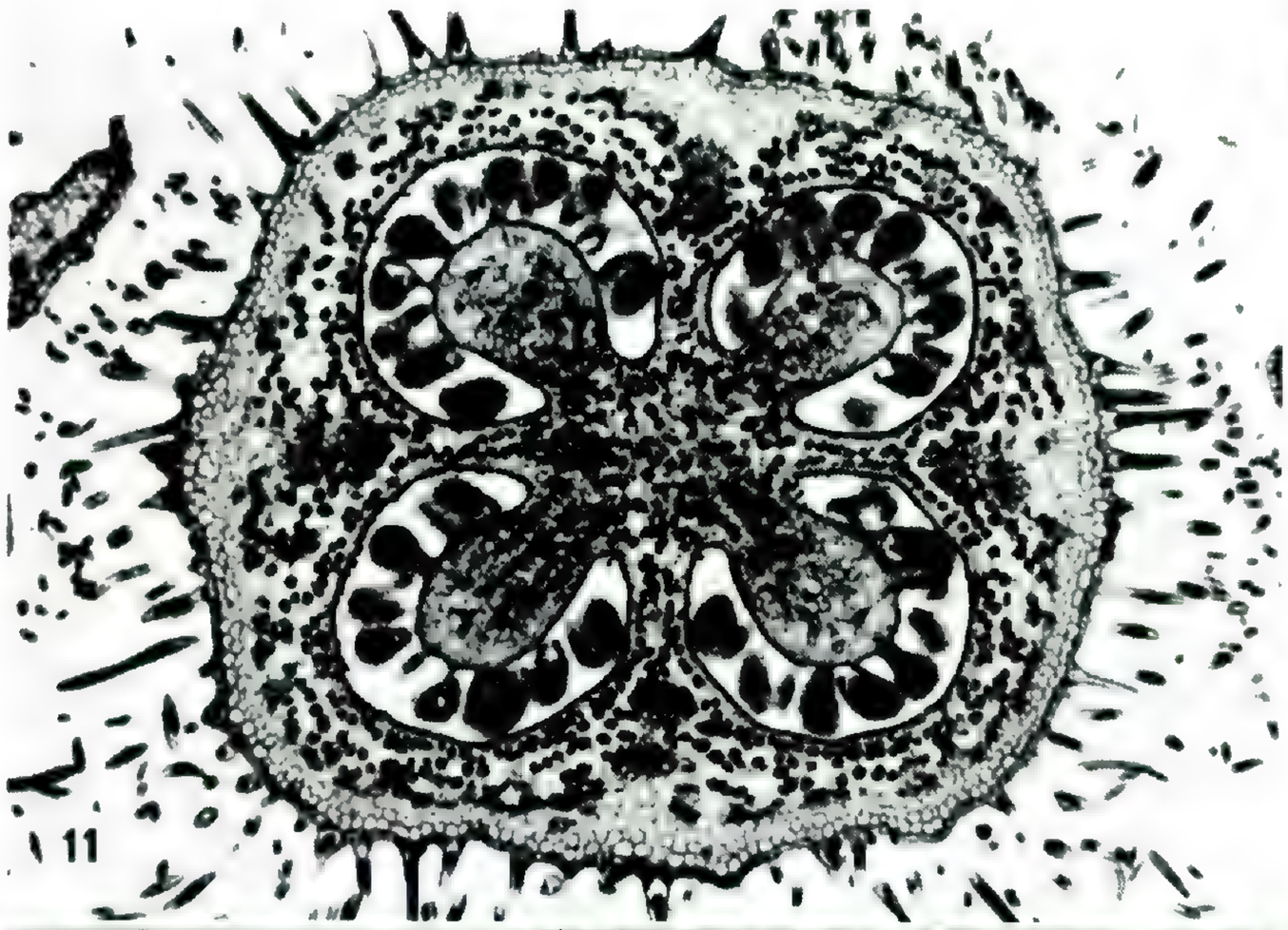
Figures 5–10. Flowers of *Ludwigia*.—5. *L. maritima* (*Arguelles 1*). Flower in longitudinal section showing abscission zone (az) at base of style (×7).—6. Another section from same series, abscission zone enlarged. Section taken just below epidermis (×95).—7–8. Similar abscission scars in sections *Ludwigia* and *Myrtocarpus*.—7. *L. maritima* (*Arguelles 1*, ×10).—8. *L. peruviana* (*Steinberg*, no number, Florida, ×7).—9. *L. virgata* (*Broome* 863). Prefertilization ovary in x.s. showing early development of spongy parenchyma. Winged ovaries are not uncommon among *Ludwigia* species (×28).—10. *L. palustris* (*Broome* 859). Immature fruit in x.s. Note thin fruit wall in locular radii (×37).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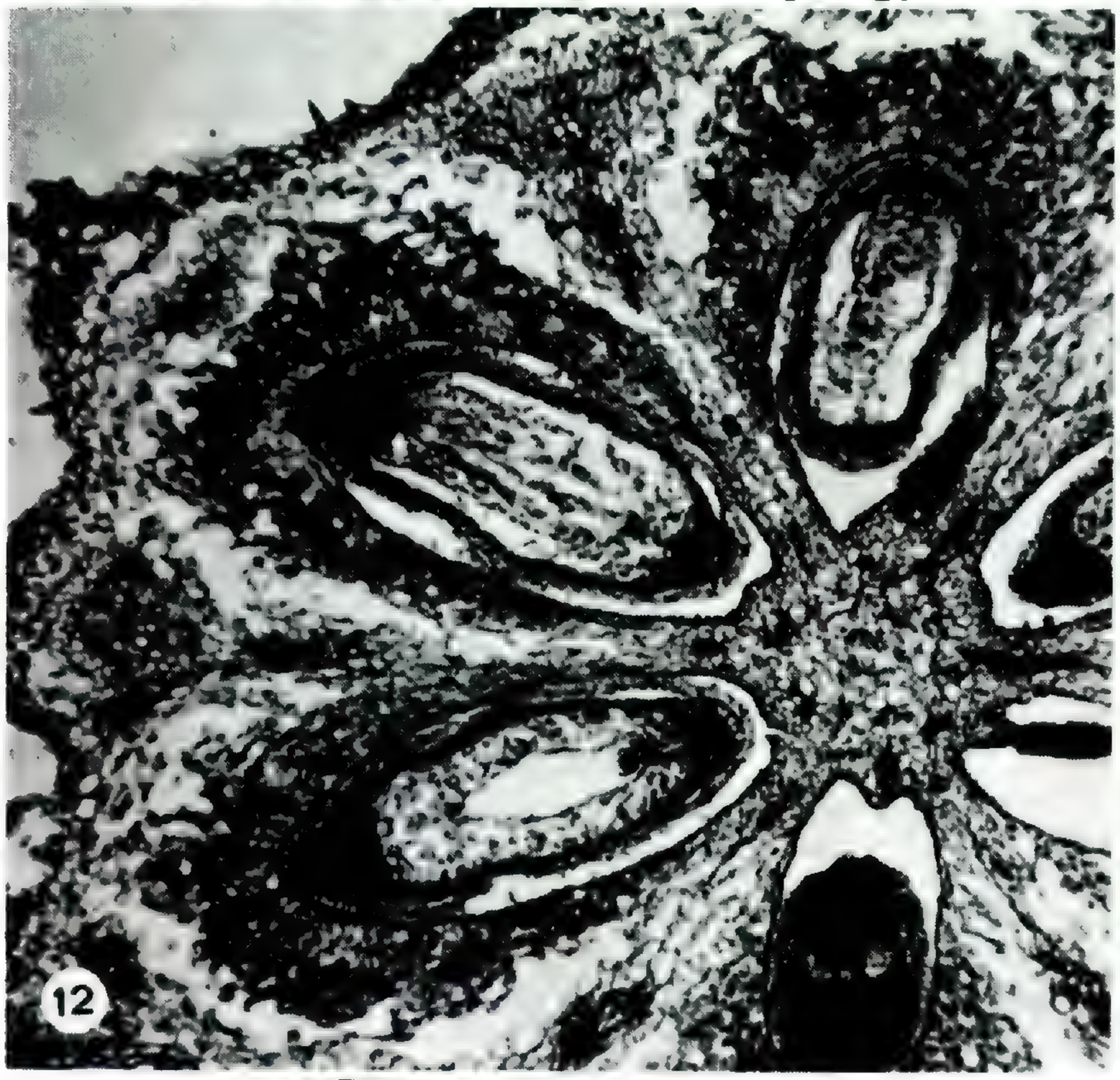
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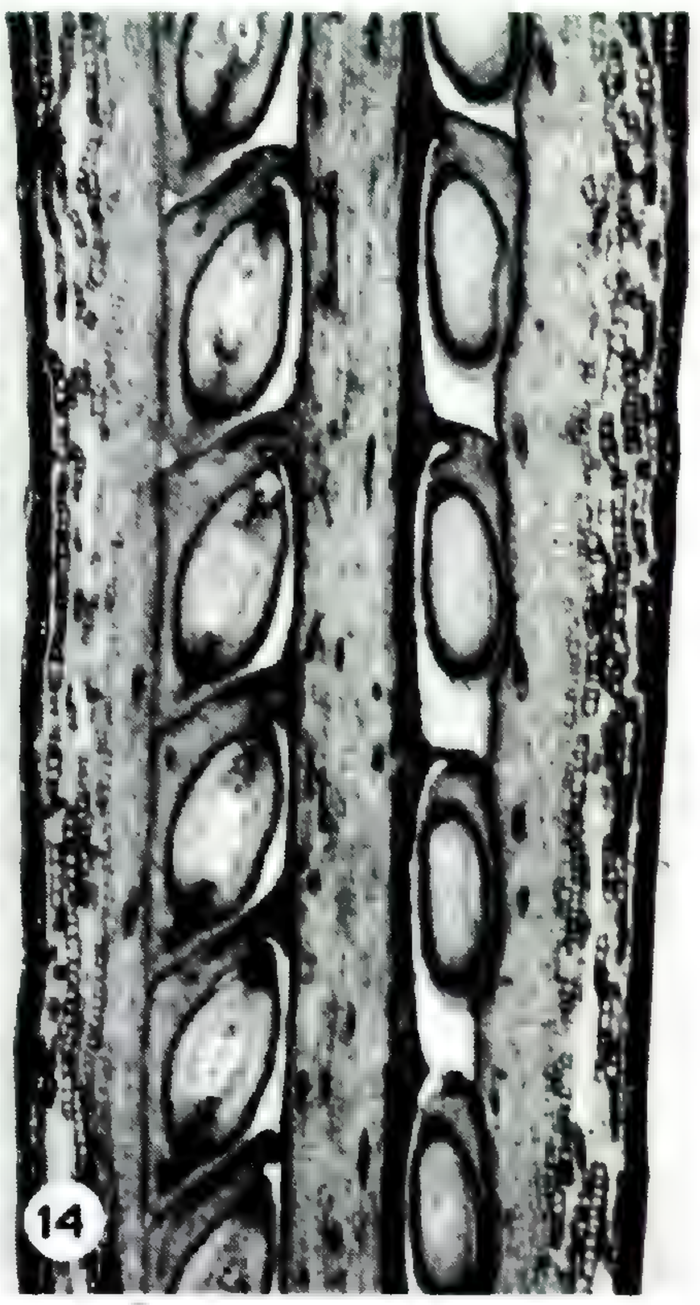
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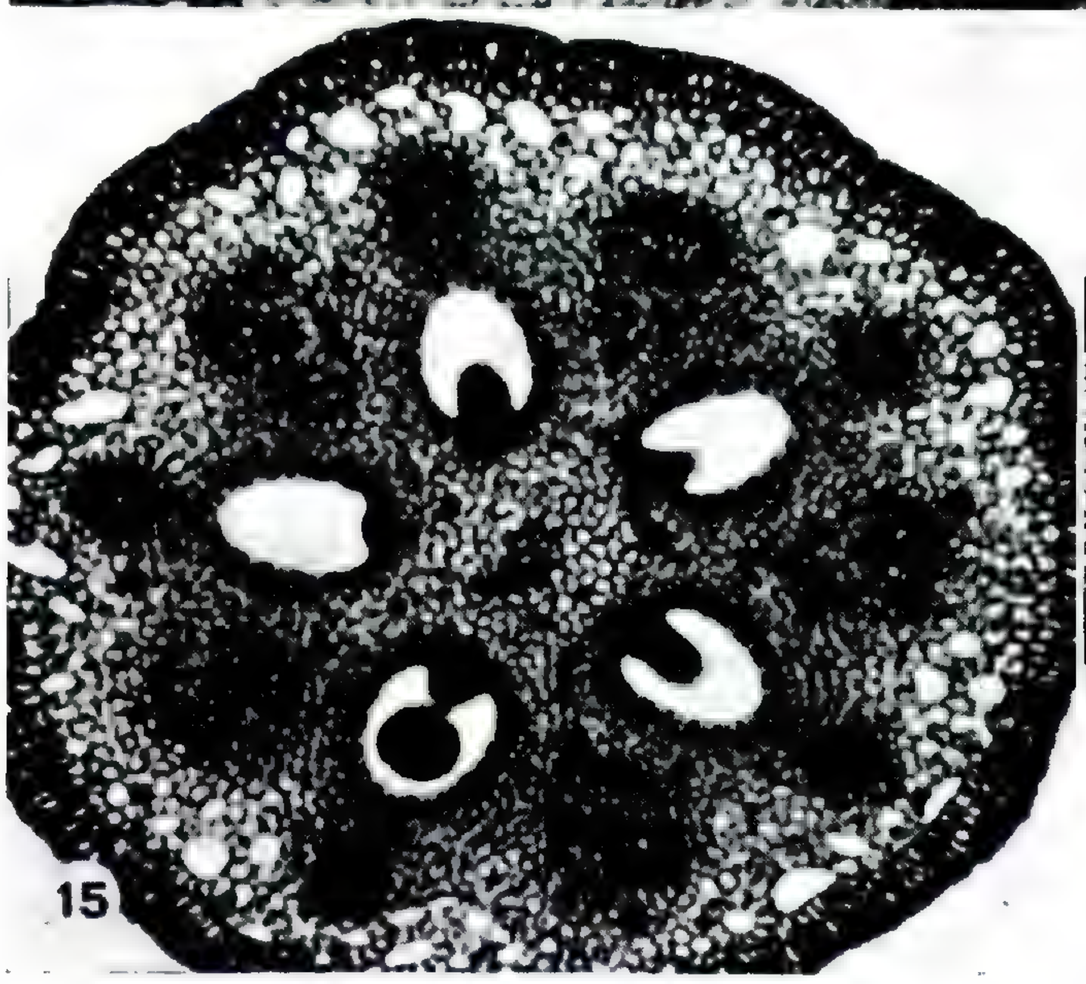
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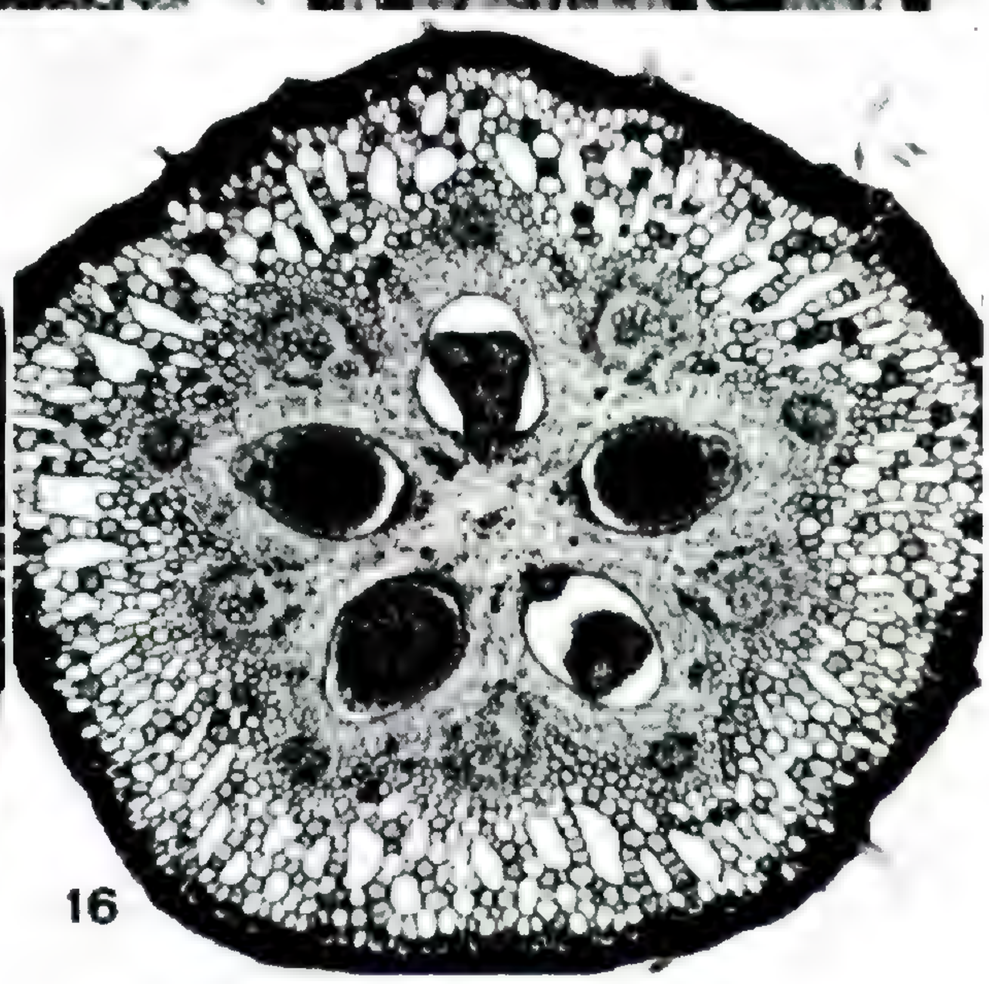
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Section *Seminuda*

Of the four species, I have worked only with *Ludwigia leptocarpa*, but my serially sectioned material of this species includes prefertilization flowers as well as fertilized ovaries at various stages of development. As in section *Macrocarpon*, the fruits are long, narrow, and cylindrical. The fruit wall parenchyma, about 10 cells thick in the intercostal areas at anthesis, has an inner lacunose zone and an outer continuous zone which separate fairly early (Fig. 12). The separation occurs several cells away from the inner epidermis, leaving more tissue attached to the epidermis than is the case in other subgeneric sections. As the fruit develops, the cells of the inner epidermis elongate into fibers, and those of the spongy parenchyma multiply. The inner zone becomes 15 or more cells thick in some places, and the spongy appearance is lost as cell divisions fill the lacunae. Cell walls thicken somewhat, and the inner zone becomes an endocarp in which the cells, except those of the epidermal layer, are isodiametric and easily separated from each other (Fig. 13). The 1-seriate seeds are larger (up to 1.4 mm long) than those of most ludwigias but do not differ histologically. They are oriented more or less horizontally, depending upon their position in the fruits, and each is loosely enclosed by its own segment of endocarp (Figs. 35–37). As was the case with *L. peruviana*, my sections suggest the loss of a third (middle) cell layer as the inner integument becomes the tegmen.

Three species outside section *Seminuda* are similar to *Ludwigia leptocarpa* in the structure of the endocarp and the orientation of the seeds. Raven's (1963) synopsis assigns each of these species to its own section. The endocarp segments of *L. abyssinica* are like those of *L. leptocarpa* in structure and color (brown), but the cross-sectional outline is triangular in the latter, horseshoe shaped in the former. The endocarp of *L. epilobioides* is white and does not develop in discrete segments, one segment to a seed; instead the endocarp can be vertically continuous through much of the ovary, and within it the seeds (Fig. 30 shows an isolated example) are often so crowded as to be almost 2-seriate. The endocarp of *L. epilobioides* is horseshoe shaped in cross-section but thinner than that of *L. abyssinica*. Endocarp segments of *L. hyssopifolia*, white and triangular, are cut through by a vascular bundle in the midplane of the locule. They therefore separate easily into halves when handled. The upper part of the fruit lacks hardened endocarp; the seeds are pluriseriate in each locule and smaller than the 1-seriate seeds below, but the large and small seeds do not differ histologically or in surface sculpture (Figs. 31–32).

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Figures 11–16. *Ludwigia*.—11. *L. pilosa* (*Broome 861*). Ovary in x.s. showing darkly stained cells in inner parenchyma layers (×37).—12. *L. leptocarpa* (*Raven 26491*). Developing fruit in x.s. showing separation of spongy parenchyma from continuous parenchyma. Inner tissues adhere to seeds at maturity (×56).—13. *L. leptocarpa* (*Proctor 16898*). Isodiametric endocarp cells, separated by maceration (×190).—14. *L. peploides* (*Raven 14529*). Postfertilization ovary in longitudinal section. Long axes of developing seeds are more nearly perpendicular than horizontal (×21).—15. *L. peploides* (*Raven 26493*). Prefertilization ovary in x.s. showing early development of intercellular spaces in outer parenchyma (×80).—16. *L. uruguayensis*. Somewhat older prefertilization ovary showing well-developed aerenchyma (×37).

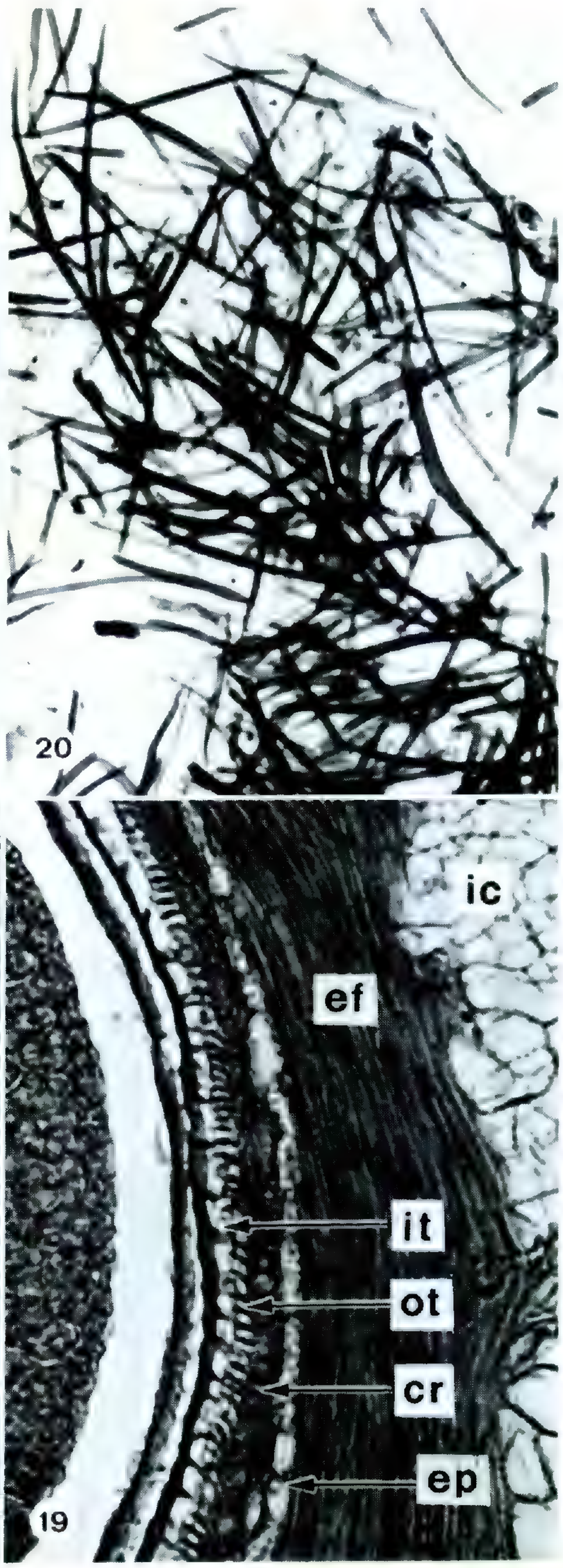
SECTION *OLIGOSPERMUM*

My sectioned material includes two of the seven species, *Ludwigia peploides* and *L. uruguayensis*. Again, the fruits are long and narrow, but the wall is somewhat thicker in flower and fruit than it is in comparable specimens from section *Seminuda*; in *L. uruguayensis*, the ovary wall can be 20 cells thick at anthesis.

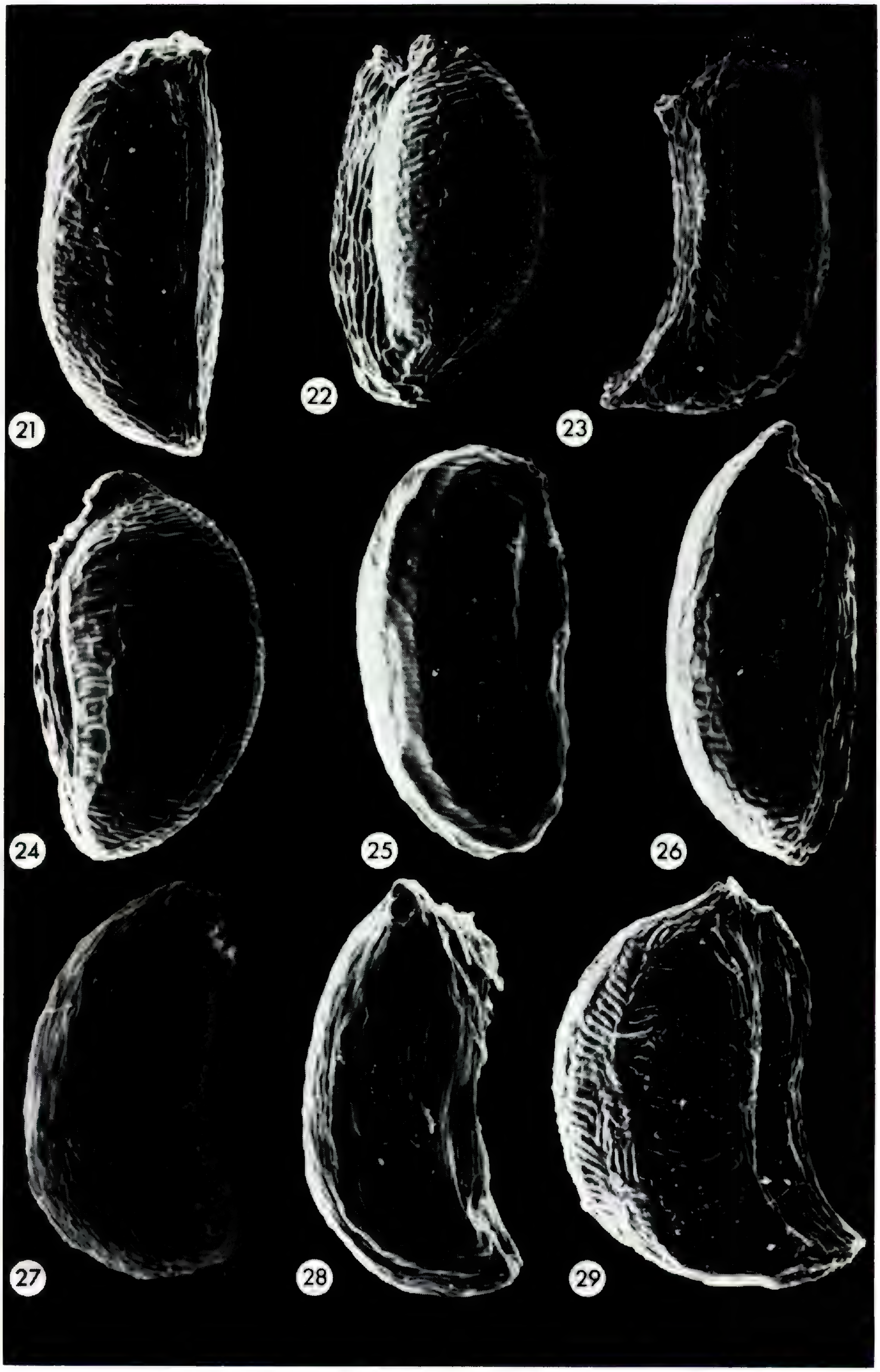
As in many other ludwigias, two tissue zones are readily distinguished. Here, however, the tissue near the outer epidermis is lacunose, becoming a well-defined aerenchyma, continuous with the cortical aerenchyma of the peduncle, before the flower opens (Figs. 15–16). Presumably, oxygen and carbon dioxide move readily between the aerenchyma of flower and peduncle, tissue of primary origin, and the aerenchyma of root and stem, tissue derived like cork from a phellogen, in the manner of the aerenchyma-mediated exchange of gases between leaves and roots. It is worth noting that Schenck (1889), who coined "Aërenchym" after studying stems and roots of *Ludwigia*, restricted the term to tissue of corklike origin. Hutchinson's (1975: 206) attempt to revive Schenck's restricted usage while using the expression "lacunar system" for similar tissue of primary origin is ill advised. If the air space tissue has a respiratory function throughout the plant, a single term reflecting that function is appropriate. Furthermore, a functional concept of aerenchyma is well based historically: Karl Goebel (1889–1893), the leading structural botanist of his time, accepted Schenck's term soon after it was proposed with the recommendation that aerenchyma be defined "nicht entwicklungsgeschichtlich, sondern biologisch."

In section *Oligospermum*, as in section *Seminuda*, the inner layers of the ovary wall develop into a discrete endocarp around each seed (Fig. 38). Here, however, the inner epidermis becomes very active after fertilization. By repeated divisions and by differentiation of the resultant cells, it eventually forms a layer of heavy-walled fibers about eight cells thick around the locules (Figs. 17–20, 40). Surrounding the fiber layers in the mature fruit are several layers of isodiametric cells much like those of *Seminuda* endocarps, but in section *Oligospermum* these cells are more or less straw colored and tend to be aligned in straighter radial files, perhaps because there is no spongy stage in the development of the *Oligospermum* endocarp.

Oligospermum seeds are like *Seminuda* seeds in size and shape, but they are positioned in the locules with their long axes more nearly vertical than horizontal (Fig. 14). A more striking peculiarity is the manner in which the growing seed fuses with the endocarp adjoining it. The union is so complete over most of the seed surface that the testa cannot be separated from the endocarp. When a seed is pried loose with forceps, cell walls are torn, mainly in the thin-walled inner layer of the tegmen. Despite this difference, the seed coats have the same four cell layers seen in other ludwigias. The outer testal layer, being the layer united with the endocarp, is modified but it is not lost; it can be traced in cross-sections if one starts at the raphe, where the seed epidermis is well defined, then advances to the septal region, where the testa and endocarp are intimately united. The crystal-bearing inner layer of the testa is the prominent layer of *Oligo-*



FIGURES 17–20. *Ludwigia peploides*.—17. *Raven 14529*. Fruit in x.s. showing endocarp tissue around each locule (×12).—18. Same, one endocarp enlarged (×47).—19. Same, further enlarged. Labels indicate isodiametric endocarp cells (ic), endocarp fibers (ef), seed epidermis (ep), crystalliferous layer (cr), outer and inner tegmic layers (ot, it) (×220).—20. *Ruth 716*. Endocarp fibers separated by maceration (×80).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spermum seed coats, as it is in other subgeneric sections, though the cells are not as large there as they are in most species. The cells of the outer tegmic layer, unlike their counterparts elsewhere in the genus, are narrower in the tangential direction than they are in the radial direction. *Ludwigia uruguayensis* ovules photographed with the aid of the Nomarski interference system show a third cell layer in the inner integument (Herr, 1973: figs. 2–3).

Fruits and seeds of *Ludwigia torulosa*, sole species of section *Oocarpon*, are structurally similar to those of section *Oligospermum* (compare Figs. 40–41), but the fruits are smaller and devoid of aerenchyma, and the seeds are fewer. I have observed a dozen or so seeds per fruit in *L. torulosa*, a hundred or more in *L. peploides*. Although the ovary wall is thinner in *L. torulosa*—about 12 cells thick at anthesis—radial divisions in the developing endocarp make the mature fruit at least as thick walled as that of section *Oligospermum*. Contours of the endocarp (Fig. 39) are rounded, with isodiametric cells more evenly distributed over the surface than is the case in *Oligospermum*.

Structure and Function

The differentiation of the fruit wall into the inner spongy zone and outer continuous zone observed in many *Ludwigia* species undoubtedly aids dispersal in that the spongy tissue is no impediment to the exit of the seeds when the capsule ripens. Though I have found nothing pertinent in works on plant evolution, I would not be surprised if it should turn out that many plants with capsular fruits have evolved the same means of reducing the effective thickness of the fruit wall. To be sure, *Ludwigia palustris* and other small-fruited species have thin walls even though there is no spongy zone. Here, however, the thin wall is linked to a difference in gynoecial vasculature that I shall treat in a subsequent article.

The appearance of the spongy zone at anthesis invites functional comparison with the spongy mesophyll of a leaf. Developing ovaries are green, and it may be that photosynthesis has a role in the differentiation of the zones. That is, photosynthesis in the outer, better-lighted cells of the ovary wall may increase their growth rate over that of the inner cells. Resultant expansion of the outer layers could pull the smaller inner cells apart to some extent and eventually separate the outer layers from the inner (Fig. 2).

It is clear enough that evolutionary alteration of the inner spongy zone to a thick endocarp of dead cells, as in section *Seminuda*, betters the floating capability of the disseminule, thereby helping the species spread from one wet area to another. But early stages in the evolutionary change—slight modifications in the inner cell layers—would not make a buoyant endocarp. Therefore, the

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Figures 21–29. Scanning electron micrographs of *Ludwigia* seeds.—21. *L. densiflora* (*Rusby 1792*, ×85).—22. *L. peruviana* (*Killip & Smith 20497*, ×55).—23. *L. latifolia* (*Gleason 676*, ×75).—24. *L. hirtella* (×85).—25. *L. palustris* (×80).—26. *L. lanceolata* (×100).—27. *L. polycarpa* (*Bissell & Clark 245*, ×115).—28. *L. glandulosa* (*Smith 1938*, ×95).—29. *L. glandulosa* (*Tracy 8496*, ×85).

initial advantage of the altered inner layers probably had to do with protection against predators. The larvae of certain insects are very destructive to *Ludwigia* ovaries (Needham, 1941; Sankaran & Krishna, 1966). Even a slight change in the spongy parenchyma would be selected for if the change made the layer less palatable at vulnerable stages in the growth of the fruit. Continued selection could produce a well-differentiated endocarp still able to discourage predation as the fruit develops, but also able to float the seeds after the fruit ripens. Needham's (1941) field observations in Puerto Rico support the suggestion that developing endocarp tissue thwarts predators. While collecting *L. octovalvis* fruits (with no endocarps) for their heavy infestation of midge larvae, he found that *L. leptocarpa* (an endocarp species) "growing along side, showed no infestation whatever."

Buoyant endocarps are not the only floating structures in *Ludwigia*. Section *Macrocarpon*'s big raphe is a float, and in at least some ludwigias the whole fruit floats. Salisbury (1972) observed, for instance, that *L. palustris* fruits can float for months, presumably because of intercellular spaces in septal radii. Seeds of this species can germinate in groups within the floating fruit or individually after the fruit has ruptured, suggesting to Salisbury the possibility of secondary dispersal in mud sticking to birds' feet. One would judge from the structure of *Oligospermum* fruits that species of this section are better adapted than *L. palustris* for two-stage dispersal. Not only does each seed have its own buoyant endocarp, but the intact fruit has a buoyant wall. It may be, however, that two-stage dispersal—floating fruit followed by floating seed—occurs only under certain conditions. I infer from the appearance of herbarium specimens that *Oligospermum* fruits ordinarily deteriorate and release seeds while still firmly attached to the plant, and Backer's (1914) field observations on *L. adscendens* say nothing about free-floating fruits.

Structure indicates a different kind of two-stage dispersal in *Ludwigia hyssopifolia*, for breakup of the fruit begins at the distal end, freeing the small upper seeds that have no endocarp covering. Subsequent deterioration frees the lower, larger seeds, each in its endocarp segment. Backer (1913) found to his surprise that both the unclad upper seeds and the endocarp-clad lower seeds float, but his experiment ended accidentally after 16 days. It is likely that the two forms would float differently if tested longer. Under natural conditions, aquatic disseminules can float off and on for months or years before germinating, and so

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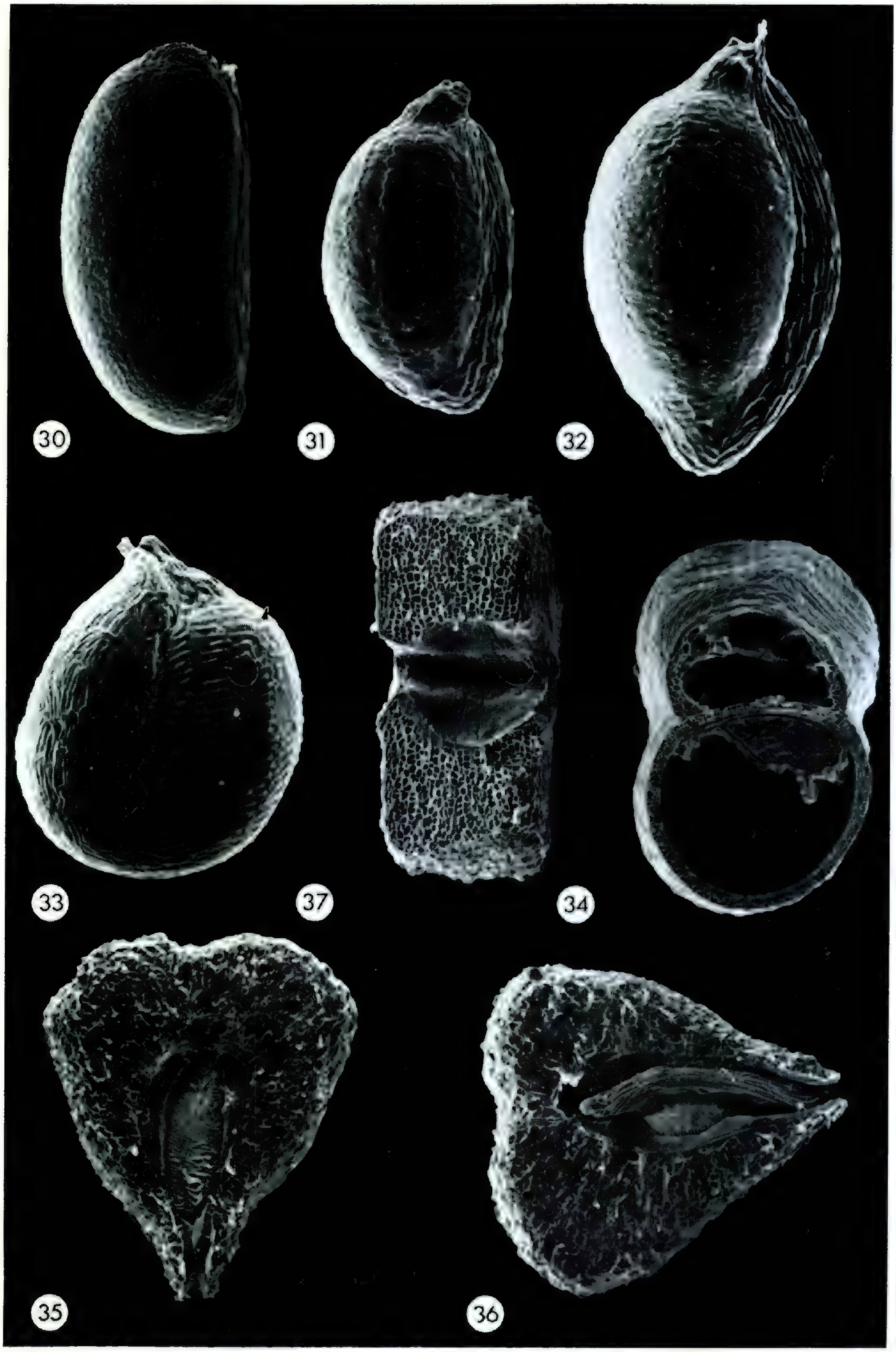
FIGURES 30–37. Scanning electron micrographs of *Ludwigia*.—30. *L. epilobioides*. Seed (×65).—31. *L. hyssopifolia*. Seed from pluriseriate region at top of fruit (×85).—32. Seed removed from endocarp segment near middle of same fruit; same magnification.—33. *L. lagunae*. Seed showing large raphe characteristic of section *Macrocarpon*. Note longitudinal ridge on each epidermal cell caused by partial thickening of outer cell wall (×90).—34. Same. Another seed cut across to show raphe's interior. Under raphe, shrunken embryo and surrounding tissue adhere to seed coats (×115).—35. *L. leptocarpa*. Endocarp segment with seed, viewed from below. Inner (fibrous) zone slopes toward seed, therefore appears thicker than it is.—36. Same. Another endocarp segment viewed from above. Note prominent raphe. Both ×35.—37. Same. Yet another endocarp segment cut to show cell structure. In this figure, long axis of fruit is parallel to width of page (×45).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many factors can affect germination (Hutchinson, 1975: 210 ff.) that one hesitates to guess at life history "strategy" without extensive experimenting. One question that could be answered with experiments: Are lower seeds better fitted to colonize partly occupied (relatively shaded) sites because they are larger and upper seeds more effective for colonizing exposed sites because there are more of them?

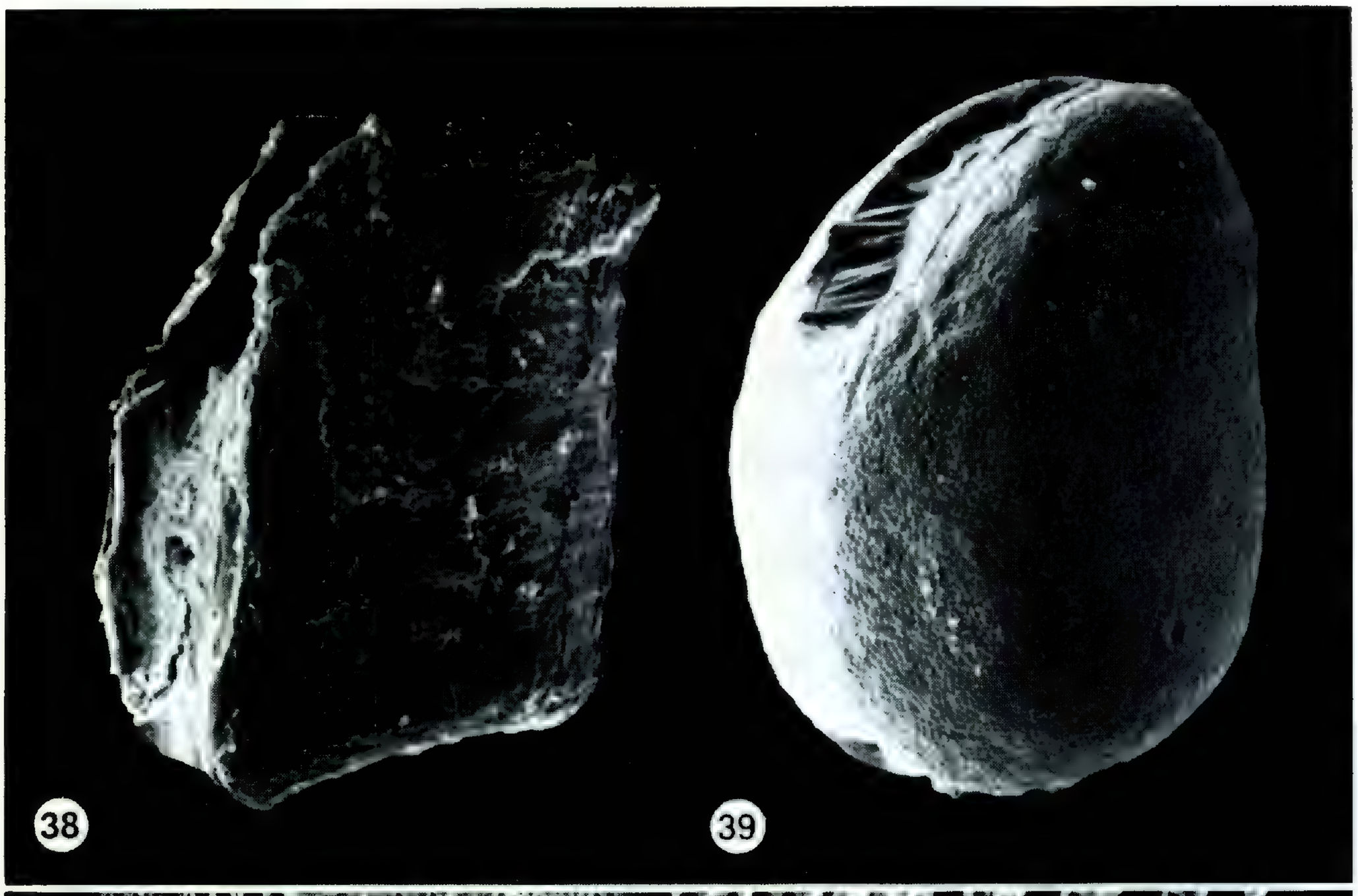
RELATIONSHIPS

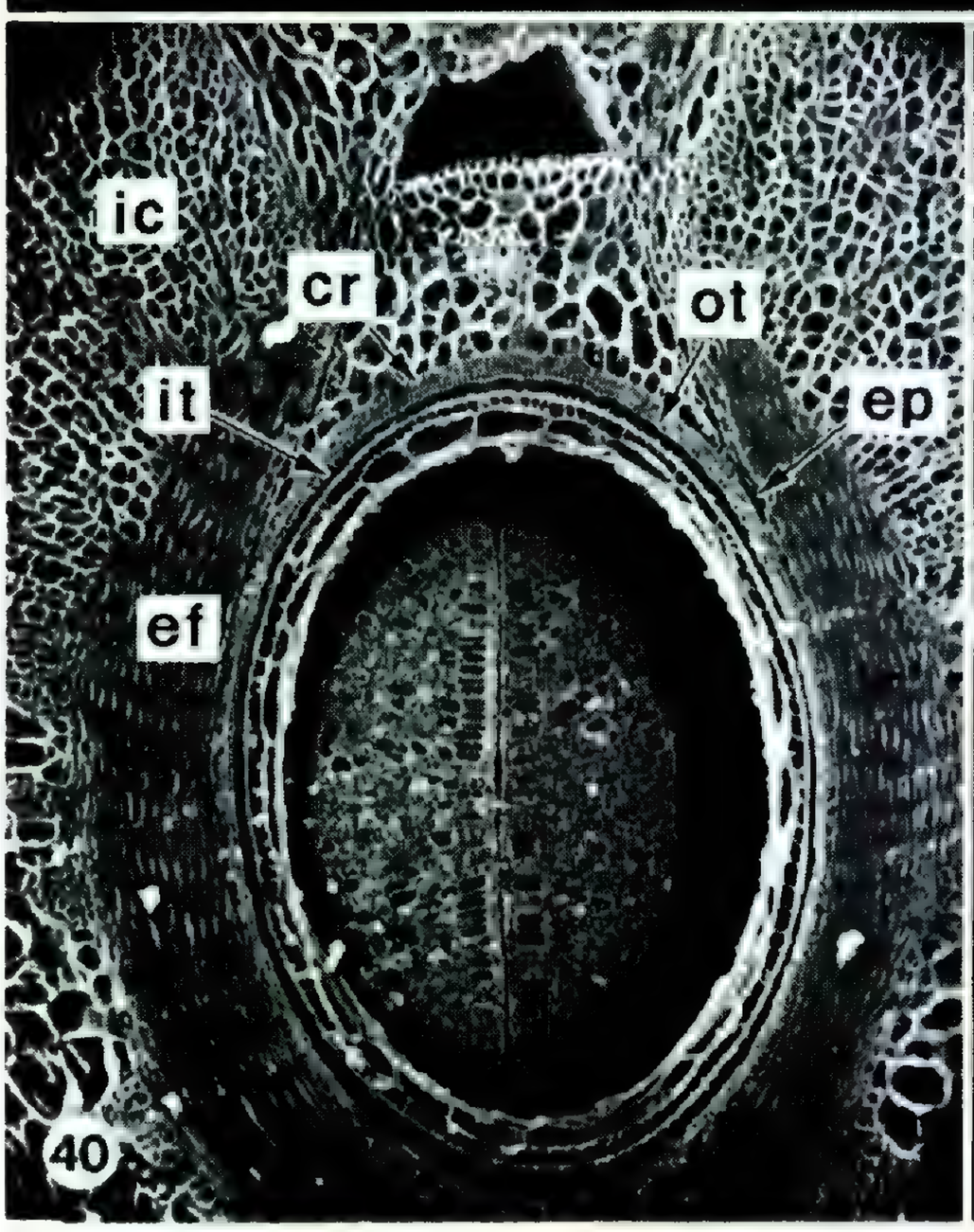
The regional monographs by Munz (1942) and Raven (1963) treat *Myrtocarpus* as the primitive section of *Ludwigia*. Floral merism, placentation, and androecial characters are consistent with this treatment (Eyde, 1977), and I have found nothing in the structure of fruits and seeds to contradict it. Indeed, the monographers had fruit characters in mind when assigning primitive status to the section: it is difficult to view a *Myrtocarpus* fruit as anything but generalized with respect to a fruit with separable endocarps. Recognizing a preponderance of ancestral features in section *Myrtocarpus* does not mean, however, that species with endocarps perforce evolved from *Myrtocarpus* species. It is more likely that two separate endocarp groups diverged from the precursors of section *Myrtocarpus*.

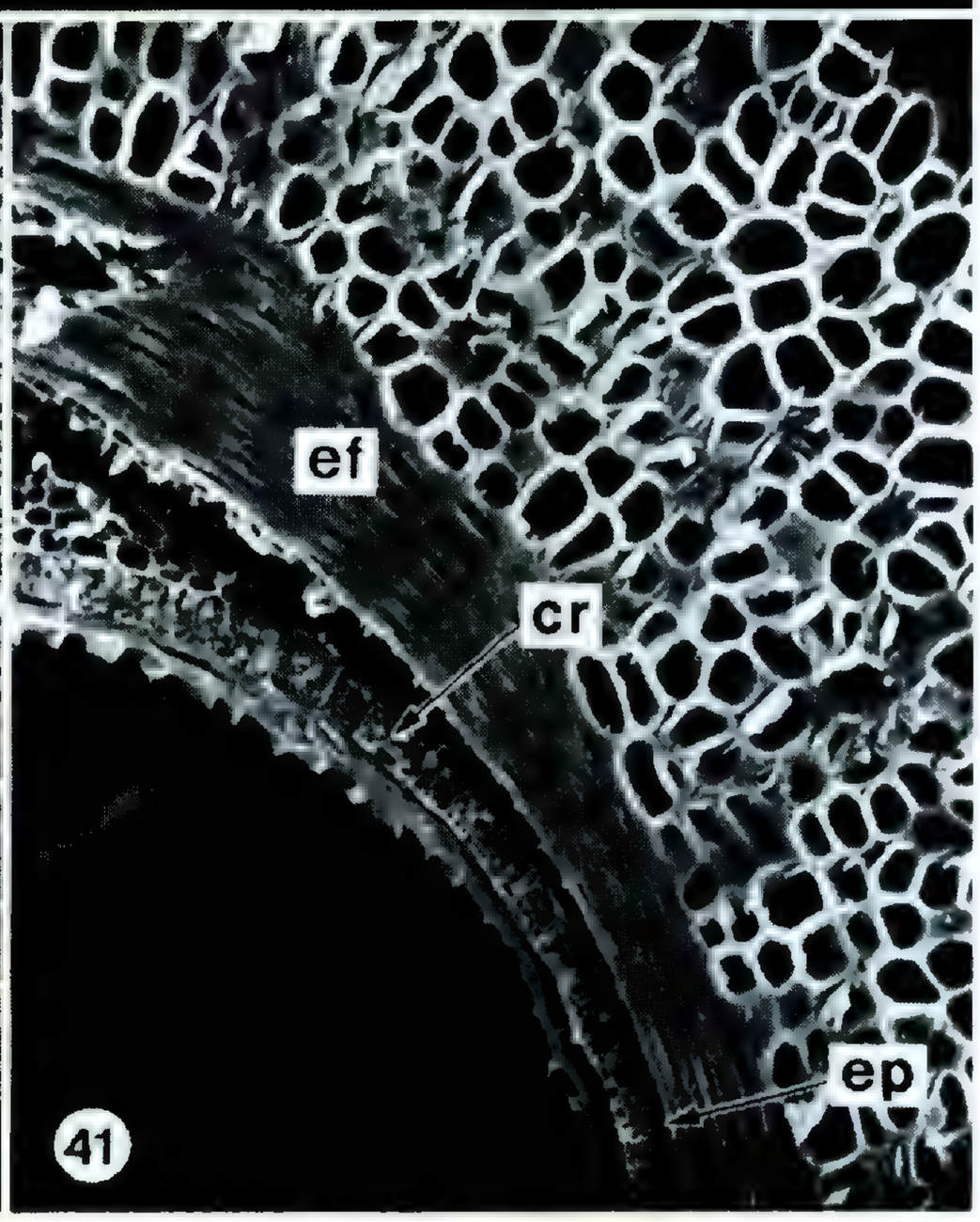
Before defending that view, I must say something on the delimitation of section *Myrtocarpus*. Raven's (1963) list of 23 species includes 2, *Ludwigia densiflora* and *L. latifolia*, that lack a well-defined spongy zone in the ovary wall. (For this reason, among others, they are to be excluded from the section in the forthcoming revision by T. P. Ramamoorthy.) I found no spongy zone in ovaries of other onagraceous genera, and this raises a question: Did the ancestors of *L. densiflora* and *L. latifolia* lose the trait, or did they diverge from other ludwigias before it evolved? When associated characters are considered—herbaceous habit and spicate inflorescence in *L. densiflora*; 4-mery, pollen packets, and adnate bracteoles in *L. latifolia*—either species seems less likely to retain an archaic feature than, say, *L. tomentosa*, a woody *Myrtocarpus* in which bracteoles are free and 5-mery is frequent. Since a spongy inner zone is evident in sectioned herbarium flowers of *L. tomentosa*, I infer that the trait was lost during the evolution of the two excluded species.

On the other hand, I see no reason to infer that *Oligospermum* ovaries ever had a spongy layer. One might envision a sequence from the mature fruit wall of section *Myrtocarpus* to that of section *Seminuda* and then to that of section *Oligospermum*, but the second step would require a major change in the histogenesis of the ovary as well as a change in the orientation of ovules. It is more likely that *Oligospermum* arose from the ancestors of *Myrtocarpus* as an offshoot with its own aquatic adaptations. If my reasoning on merism (Eyde, 1977) is right, *Seminuda* probably diverged later from the same ancestral line after the ovaries had acquired the inner spongy zone, but before the widespread stabilization of 4-mery.

Endocarp histology confirms the close kinship of *Ludwigia torulosa* to section *Oligospermum*, though fruit wall aerenchyma is lacking in *L. torulosa*. It is far







FIGURES 38–41. Scanning electron micrographs of *Ludwigia*.—38. Endocarp of *L. peploides*. In intact fruit, raphe descends through apical cavity and large longitudinal vascular bundle occupies dorsal groove to left (×35).—39. Endocarp of *L. torulosa* (×45).—40. *L. peploides* (*Raven 14529*). Part of liquid-preserved fruit cut across to show seed with surrounding endocarp. Labels as in Figs. 4, 19. Though specimen was prepared by critical point drying, shrinkage of cotyledons is evident (×80).—41. *L. torulosa*. Herbarium endocarp with adhering seed coats, x.s. Thin seed epidermis can be traced upward in figure to multilayered region on raphe side where seed has separated from fruit wall. Note torn cells between endocarp fibers and crystalliferous layer (×190).

from clear, however, that all species with endocarp segments forming from spongy parenchyma have a close common ancestry. For one thing, endocarp segments are brown in some of these species, white in others. The color difference need not be an indication of remoteness if we recall that *L. pilosa* has a darker inner zone than its relatives in section *Microcarpium*. More important are the indications that in *Ludwigia* an endocarp *must* develop whenever selection brings about a 1-seriate arrangement of ovules.

Seeds forming in a single file establish extensive surface contact with the ovary wall, and morphogenic substances produced by the growing seed can then diffuse into the ovary's inner layers, converting them to endocarp much as integuments are converted to seed coats. I have not tested the phenomenon biochemically, to be sure, but the pattern of endocarp formation around each seed is clear-cut. Narrow segments of fruit wall opposite the gaps between ovules receive less of the diffusing substance(s); that is why there are discrete endocarp bodies around each mature seed—except in *L. epilobioides*. In that species the ovules are crowded, rather than 1-seriate; so the endocarp is vertically continuous. Given the ontogenetic link between 1-seriate seeds and endocarp formation in *Ludwigia*, it follows that a similar evolutionary sequence may have occurred more than once within the genus: hemispherical or obconical fruits with pluriseriate seeds, then longer fruits with fewer seeds per cross-section, finally linear fruits with 1-seriate endocarp-clad seeds. Selective pressure for the initial change lay in the ability of a long, narrow fruit to function as an extension or replacement for the peduncle. The adaptive value of a neat 1-seriate arrangement lies in its link with endocarp formation, perhaps also in the fact that the evolutionary reduction of the placenta deprives larvae of a choice feeding site (see Needham, 1941). A disadvantage that must be offset by a lineage following this route is the decrease in number of seeds per fruit. *Ludwigia hyssopifolia* is an evolutionary compromise in that the upper part of the fruit retains the ancestral condition.

Fruits of sections *Ludwigia* and *Macrocarpon* are enough like those of section *Myrtocarpus* to suggest direct derivation from *Myrtocarpus*; however, Ramamoorthy tells me he presently favors the derivation of *Macrocarpon* from extinct ancestors of *Myrtocarpus*. The derived sections retain the spongy zone in the fruit wall, but each has its own advanced traits: in *Macrocarpon*, enlarged raphes and narrower, more heavily ribbed and more readily ruptured fruits; in section *Ludwigia*, haplostemony and poricidal fruits, the latter "foreshadowed" by some *Myrtocarpus* fruits (p. 661). Though sections *Dantia* and *Microcarpium* do not have a well-developed spongy parenchyma, they probably arose from *Myrtocarpus*, perhaps as one lineage. Links between these two sections and between *Microcarpium* and *Ludwigia* may be clarified when *Microcarpium*, now under study by David Dille at the Missouri Botanical Garden, is revised. *Dantia* has been shown to be a polyploid complex of five species, close enough to at least two species of *Microcarpium* for natural intersectional hybridization to occur (Schmidt, 1967). *Microcarpium*, judged by the differences in surface cell orientation of the seeds, is remarkably diverse. The differences may be species-specific, despite the apparent heterogeneity within *L. glandulosa* (*Tracy 8496* vs. *Smith*

1938). Munz (1944) accepted *Tracy 8496* as *L. glandulosa*, but the fruits are unlike those of other *L. glandulosa* specimens in the US collection.

The third and final paper of this series will describe floral vasculature and summarize suggested evolutionary links in a diagram.

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POLLIA THUNB. (COMMELINACEAE): THE FIRST GENERIC RECORD FROM THE NEW WORLD

Robert B. Faden[1]

Abstract

A collection from Panama, representing the first New World record of *Pollia*, is described as *P. americana* Faden. The plant appears to be indigenous.

The genus *Pollia* Thunb. (including *Aclisia* E. Mey.) is widely distributed in the tropics and subtropics of the Old World. Approximately 12 species occur from India and Sri Lanka to China, Japan, Malaysia, the Philippines, New Guinea, eastern Australia, and the Solomon Islands. Another four are confined to tropical Africa, including Madagascar. In 1974 I received for determination a fruiting specimen from Panama (*Gentry 3806*) which clearly belonged to this genus and embodied the first New World record of it. The specimen appeared to represent an undescribed species, but as I had not seen material of some *Pollia* taxa, I hesitated to describe a new one. In 1976 I was able to study specimens of the remaining species in the genus at the Royal Botanic Gardens, Kew, and Muséum National d'Histoire Naturelle, Paris, and to confirm that the Panamanian plant is not conspecific with any described species.

Pollia americana Faden, sp. nov.—Fig. 1.

Herba foliis anguste ellipticis ad oblanceolato-elliptica, (15–)23–30 cm longis, (5–)6.5–7.5 cm latis. Inflorescentiae thyrsi terminales, pedunculati, anguste ovoidei, 14.5–16 cm longi, 8–9.5 cm lati, cincinnis ca. 50–62 pro parte maxima subverticillatis compositi. Cincinni ascendentes, 2–5.5 cm longi, 2–8 flores efferentes, dense puberuli. Pedicelli frugiferi erecti ad ascendentes, 4–5.5 mm longi. Fructus bacciformes, indehiscentes, sphaerici, cyanei, 5.5–7 mm diametro. Semina biseriata, 2–5 in quoque loculo, 8–12 in quoque fructu, 2.6–3.1 mm diametro, hilo lineari, 0.5–0.75 mm longo.

Herb ca. 0.5 m tall. Leaves (except the uppermost, reduced ones on the peduncle) petiolate; sheaths overlapping, 2–3 cm long, puberulous-scabrid with hook-hairs (terminology of Tomlinson, 1966), not ciliate at the apex; laminae narrowly elliptic to oblanceolate-elliptic, (15–)23–30 cm long, (5–)6.5–7.5 cm wide, the apex acuminate, the base attenuate, both surfaces puberulous-scabrid, the adaxial with prickle hairs, the abaxial with hook-hairs, the margins scabrid with prickle hairs, especially towards the apex; petioles not undulate. Inflorescences solitary, terminal, pedunculate thyrses, the peduncles robust, 14–16 cm long, bearing 1–2, spaced, reduced, sessile leaves, densely puberulous with hook-hairs; thyrses narrowly ovoid, 14.5–16 cm long, 8–9.5 cm wide, with ca. 50–62, mostly subverticillate, ascending (or the uppermost patent) cincinni; inflorescence axis densely puberulous with uniform-length hook-hairs; cincinnus bracts herbaceous, lanceolate, 4–10 mm long, reflexed, mostly persistent, sparsely puberulous

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Ann. Missouri Bot. Gard. 65: 676–680. 1978.

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FIGURE 1. Holotype of *Pollia americana* Faden, *Gentry 3806* (MO).

abaxially; cincinni 2–5.5 cm long, 2–8 flowered; cincinnus peduncles 7–17 mm long, the longest in the lower cincinni, decreasing upwards, densely puberulous with uniform-length hook-hairs; cincinnus axis slightly undulate between the bracteoles, densely puberulous with uniform-length hook-hairs; bracteoles spaced 4–8 mm apart, cup-shaped, perfoliate (occasionally splitting to the base), more

or less herbaceous, 2.5–4 mm long, not evidently glandular, puberulous, especially towards their bases. Flowers unknown. Fruiting pedicels ascending to erect, 4–5.5 mm long, glabrous or sparsely puberulous. Sepals persistent and reflexed in fruit, convexo-concave, ca. 4 mm long, glabrous or very sparsely puberulous. Fruits bacciform, indehiscent, spherical, 5.5–7 mm in diameter, lustrous, pale blue with darker blue patches, cells of the outer wall mostly transversely elongate. Seeds biseriate, 2–5 per locule, 8–12 per fruit, triangular to polygonal in outline, dorsoventrally flattened, 2.6–3.1 mm in diameter, testa grey brown, finely pitted, embryotega concolorous, hilum linear, 0.5–0.75 mm long.

TYPE: PANAMA. PANAMÁ: Ca. 16 km from Río Bayano on trail to Santa Fé, herb 0.5 m, fruits blue black, 25 Jan. 1972, *A. Gentry 3806* (MO, holotype; BM, isotype).

RELATIONSHIPS

The relationships of *P. americana* are difficult to assess. This is due largely to the ambiguity regarding which characters are indicative of affinity in this genus. I have previously noted that the use of certain attributes to delimit sections of *Pollia*, e.g., number of fertile stamens (Clarke, 1881), has resulted in apparently unnatural sections, and that no satisfactory division of the genus has been proposed (Faden, 1975). The lack of flowers in *Gentry 3806* prevents its placement to section in any published scheme.

Pollia americana is highly distinctive because of its large, hairy leaves, large, robust inflorescences with numerous, mostly subverticillate cincinni, widely spaced bracteoles, and large seeds (apparently the largest in the genus). It is most similar to *P. hasskarlii* Rolla Rao (Himalayas to Java), *P. japonica* Thunb. (Japan to China), *P. macrophylla* (R.Br.) Benth. (Philippines to Australia), *P. verticillata* Hall. f. (New Guinea), and *P. gracilis* C. B. Clarke var. *madagascariensis* H. Perr. (Madagascar) in inflorescence form and cincinnus arrangement. *Pollia hasskarlii* departs from *P. americana* in its undulate petioles, smaller inflorescences, caducous cincinnus bracts, bracteoles and sepals, densely puberulous sepals, more isodiametric cells of the outer fruit wall, and smaller seeds; *P. japonica* differs in its longer-pedunculate inflorescences with more widely separated whorls of cincinni, less widely spaced bracteoles, shorter fruiting pedicels, and smaller seeds; *P. macrophylla* contrasts by its smaller, glabrous laminae, smaller, less robust, more shortly pedunculate inflorescences, longer, decurved fruiting pedicels, narrower, ellipsoid, plumbeus fruits, and smaller seeds with a smooth, grey testa; *P. verticillata* diverges in its smaller leaves with caudate apices, smaller, less robust, more shortly pedunculate inflorescences, longer fruiting pedicels, deciduous sepals, and smaller seeds with a smooth, grey testa; *P. gracilis* var. *madagascariensis* differs in its less robust inflorescences, narrower, ellipsoid, grey brown fruits, and apparently smaller seeds (only immature seeds seen).

DISCUSSION

Pollia americana appears to be indigenous in Panama. Recent introduction would seem to be ruled out by its distinctness from all Old World species. Its

undisturbed rain forest habitat also suggests nativeness. A number of *Pollia* species are widely distributed on islands and are evidently easily dispersed long distances. This dissemination is probably enhanced by birds eating the berrylike fruits. Thus the spread of *Pollia* to the New World can readily be explained by natural dispersal.

In addition to *Pollia*, only five other genera of Commelinaceae (out of the approximate 45 in the family) have indigenous species in both the New and Old Worlds: *Aneilema* (1 of its 60 species in the New World), *Buforrestia* (1 of 3), *Commelina* (ca. 15–20 of ca. 200), *Floscopa* (3–4 of ca. 20), *Murdannia* (4 of 40–45). *Pollia* agrees with all of them in having the bulk of its species in the Old World. It is most like *Murdannia* in having its main center of diversity in tropical Asia, while the other four genera are exclusively (*Buforrestia*) or predominantly African.

All six of these genera appear to have been dispersed from the paleotropics to the neotropics. This is implied by the greater number of Old than New World species in all of them. It may also be inferred from the fact that the closest relationships of all these genera, except *Commelina*, are with strictly Old World genera. Even *Commelina* appears to have been an offshoot of the evolutionary line which produced *Spatholirion*, *Streptolirion* and *Aëtheolirion*, all Asiatic genera, while the genera of closest affinity to *Commelina*, the neotropical *Phaeosphaerion* and *Commelinopsis*, are evidently derivatives from it, and probably arose subsequent to its dispersal to the New World. Studies at the species level are sufficiently advanced only in *Aneilema* to shed some light on the question of geographic origin. The single neotropical species, *A. umbrosum* (Vahl) Kunth, is part of a species complex centered in West Africa and clearly has reached the neotropics in relatively recent times (Faden, 1975).

The American distributions of the amphi-Atlantic genera of Commelinaceae suggest in most cases dispersal from the paleotropics to South America. The indigenous American species of *Murdannia* and *Buforrestia* are strictly South American; *Aneilema* reaches western Panama at its northern limit; *Floscopa* has all its species in South America, with one extending to Nicaragua. *Commelina* has reached the New World at least twice and is well represented in both North and South America. Our knowledge of its species is too incomplete to determine where they might first have arrived in the New World. *Pollia* is the only one of these genera not known from South America. Its eastern Panamanian distribution, however, suggests that it may occur in the poorly known, adjacent part of that continent.

The discovery of *Pollia* in the New World represents a remarkable range extension. It is now added to a growing list of amphi-Atlantic genera once considered restricted to the Eastern or Western Hemispheres: *Maranthes* (Chrysobalanaceae; Prance, 1968), *Hymenaea* (Leguminosae, Caesalpinoideae; Lee & Langenheim, 1975), *Commiphora* (Burseraceae, Gillett, personal communication).

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A REVISION OF THE GENUS *BORRICHIA* ADANS. (COMPOSITAE)[1]

JOHN C. SEMPLE[2]

ABSTRACT

Borrichia Adans. (Compositae: Heliantheae) is a small North American genus of two well-collected species and their hybrid and one species known only from the type collection. *Borrichia frutescens* (L.) DC. grows in saline habitats along the Atlantic and Gulf coasts from Virginia to the Yucatán. *Borrichia arborescens* (L.) DC. occurs along the coasts of the northern West Indies and tropical Florida where it hybridizes with *B. frutescens*. The hybrids were first described as a species *B.* × *cubana* Britton & Blake (pro sp.). *Borrichia peruviana* DC. is known from the vegetative type collection. *Borrichia demissa* DC. has been excluded from the genus.

The only comprehensive treatment of the genus *Borrichia* DC. (Compositae, Tribe Heliantheae) the "Sea Ox-eye Daisy" was that of de Candolle (1836: 488–489). Since then several species have been described and the entire field of modern biosystematics developed. I have reviewed the chromosomal biology of the genus (Semple, 1978), and a detailed study of Floridian populations of *B.* × *cubana* Britton & Blake (pro sp.) has been made (Semple & Semple, 1978). The number of estimated species has been reported recently as seven by Willis (1966: 148) and Long & Lakela (1971: 833–834) and five by Gleason (1952: 339) and Correll & Johnston (1970: 1644–1645). This paper reviews the pertinent literature on the taxonomy of the genus and provides species descriptions and a key to the revised genus.

NOMENCLATURAL HISTORY

Linnaeus (1753: 903) first described the type species as *Buphthalmum frutescens* L. from New World collections from Virginia and Jamaica and associated the species with the Old World taxon *Buphthalmum salicifolium* L. (designated type of *Buphthalmum*). Later, Linnaeus (1759: 1227) split *B. frutescens* into two species, with the Jamaican collection included in *B. arborescens* L. De Candolle (1836) recognized the significant differences between the Old World species, members of the Tribe Inuleae, and the New World species, and he placed the latter in *Borrichia*, a name proposed by Adanson (1763: 130) to honor the seventeenth century Danish botanist Ole Borch. Adanson did not list any species in his genus, however. De Candolle (1836) remedied this and in addition to the two Linnaean species which he transferred to *Borrichia*, *B. frutescens* and *B. arborescens*, he included three more species: *B. peruviana* DC., *B. argentea* DC. and *B. demissa* DC. De Candolle listed synonyms for the five

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[1] This work was primarily done while I was a student and research associate at the Missouri Botanical Garden. Financial support during the latter phases of the work was through an operating grant from the National Research Council of Canada. Comments on the manuscript and help on typification by Dr. William G. D'Arcy of the Missouri Botanical Garden were appreciated.

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ANN. MISSOURI BOT. GARD. 65: 681–693. 1978.

0026-6493/78/0681–0693/$01.45/0

species, as well. Of the three additional species only one, *B. peruviana*, is treated as distinct in this revision. The type collection is unfortunately vegetative only and little can be said about the taxon. The second species has been placed in synonymy under *B. arborescens* in this revision, while the third species *B. demissa* has been excluded from *Borrichia* based on fruit morphology.

Small (1903: 1262–1263) described another species, *B. glabrata* Small, from *Curtiss 1412* collected in tropical south Florida. In the 1915 edition of the *Flora of the Southeastern United States*, however, Small placed *B. glabrata* in synonymy under *B. arborescens*, having studied the species from locations other than the Florida keys.

The last species to be described was *B. cubana* Britton and Blake (Britton, 1920) based on a Cuban collection, *León 7244*. No further collections of this species were correctly identified except for those of Ekman from the same location several years later. My research has discovered ten more collections of this species made in the Florida Keys during the last 75 years by several botanists, including Small. Several extensive populations of the taxon were also located during June of 1975.

The status of each taxon was investigated through field work, chemical and cytological studies, experimental greenhouse studies when possible, and examination of herbarium specimens from the following herbaria: BUS, F, FAU, FLAS, FSU, GH, IJ, MO, MSC, SMU, TEX, TUFTS, US, USF, and WAT. The curators of these institutions are thanked for their cooperation.

SYSTEMATIC TREATMENT

Borrichia Adans., Fam. Pl. 2: 130. 1763. Based on Dillenius Etham. *tab.* 83, *fig. 43* = *B. arborescens*; *fig. 44* = *B. frutescens.*

Diomedea Cass., Bull. Sci. Soc. Philom. Paris 1817: 70. 1817. TYPE: *D. bidentata* Cass. = *Borrichia frutescens* (L.) DC.

Soboliferous or fruticose *perennials* to 1.5 m tall; roots fibrous, at times adventitious; stems woody, decumbent to erect, branching, the sap sticky resinous. *Leaves* opposite, heteroblastic; primary stem leaves petioled to nearly sessile, occasionally serrate-dentate; secondary branch leaves progressively more linear-oblanceolate, entire and reduced in size, 2–10 cm (rarely more) long, glabrous to pubescent, firm, coriaceous or succulent, mucronate, the teeth often spinulose. *Inflorescence* terminal solitary heads or a few heads clustered on short lateral branches. *Heads* globose to turbinate; phyllaries in 2–3 series, the outer ones larger and decussate, ovate with a spinulose tip or merely acute-cuspidate, 10–45; receptacle slightly convex, the paleas partially enclosing fruit, resembling the inner involucral bracts; ray florets pistillate, yellow, the strap ovate, the apex notched; disc florets perfect, yellow, tubular, the anthers black with orange connective glands, the style bifurcate, terete, the style branches papillate. *Fruits* (cypselas) of the periphery laterally compressed, appearing 3-angled, transversely depressed obtrullate in cross-section, those of the center 4-angled, tapering at base, rhombic in cross-section, gray to black, glabrous, faintly finely reticulate; pappus a 3–4-angled united crown, straw colored, occasionally deciduous on older fruits after release from head. Chromosome number: $x = 14$, $n = 14$.

Lectotype species: *Borrichia frutescens* (L.) DC.

As delimited in this revision, *Borrichia* includes shrubs with opposite leaves and yellow-flowered, essentially solitary, radiate heads. The diagnostic character is the achene pappus, which is straw colored and forms a 3–4-angled united crown on the black 3–4-angled achene. The leaves of the plant are used as a medicinal tea in the Bahamas (Eldridge, 1975).

KEY TO THE TAXA OF *BORRICHIA* IN NORTH AMERICA AND THE WEST INDIES

a. Involucral bracts obtuse to acute, not spinulose tipped; leaves of mature plants entire, glabrous or sericeous; chaff paleas papery, the apex obtuse or acute ---------- 2. *B. arborescens*

aa. Involucral bracts prominently spine tipped; leaves of primary branches serrate or dentate, villous-sericeous (rarely coriaceous and glabrous).

b. Involucral bracts long spinulose tipped, often strongly reflexed; primary and secondary branch leaves mostly with large petiolar spines; chaff paleas folded, spinulose tipped ---------- 1. *B. frutescens*

bb. Involucral bracts cuspidate, not reflexed nor swollen in fruiting heads; primary and secondary branch leaves serrate or dentate along the mid portion of the blade only, often undulate and coriaceous; chaff paleas cuspidate tipped ---------- 3. *B.* × *cubana*

NOT INCLUDED IN KEY: 4. *B. peruviana*, known only from the vegetative type collection. See text.

1. **Borrichia frutescens** (L.) DC., Prodr. 5: 488. 1836.

Buphthalmum frutescens L., Sp. Pl. 903. 1753. TYPE: Virginia (?BM, not seen).
B. incanum Mill., Gard. Dict., ed. 8. 1768. TYPE: Bahamas (not seen).
Diomedia bidentata Cass., Dict. Sci. Nat. 13: 283. 1819. Based on *Buphthalmum frutescens* L.
Borrichia frutescens (L.). DC. var. *angustifolia* DC., Prodr. 5: 489. 1836. TYPE: Mexico, Tampico, *Berlandier 126* (G, seen on microfiche).

Soboliferous perennials, forming dense clones, overwintering by rhizomes, *fruticose perennials* in areas without killing frosts. *Leaves* heteroblastic villous-sericeous; primary branch leaves petiolate, obovate to elliptic, the apex acute or mucronate, the margins basally serrate-dentate spinulose (rarely along most of margin), the blade attenuate, the petiole with one or more pairs of large spinulose teeth near the base; secondary branch leaves becoming progressively more sessile, entire, oblanceolate-linear, the apex acute or mucronate. *Heads* solitary, terminal and on lateral branches near the shoot apex, globose; peduncles 2–6 cm long; phyllaries in 3–4 unequal series, 20–40, the outer shorter, 2–4 mm long, the apex obovate with a woody recurved spine, the inner similar with the spines spreading to erect, 3–6 mm, sericeous except for the spines; receptacle slightly convex, the chaff folded, oblanceolate, 4–6 mm long, with a long orange yellow, woody spine 1.5–3 mm long, becoming thickened with age; ray florets pistillate, fertile, yellow, 15–30; disc florets perfect, fertile, yellow, 20–75. *Fruits* (cypselas) black at maturity, 3–4 angled, the peripheral ones traversely depressed obtrullate in cross-section, the inner rhombic in cross-section, 2.5–4(–5) mm long; pappus a 4-angled united crown, straw colored. Heads disintegrating after one or more seasons, globose, the outer phyllaries fully reflexed due to the thickening of the phyllaries, chaff, and fruit. Chromosome number: $n = 14$ (rarely $3x$).

DISTRIBUTION AND HABITAT

Borrichia frutescens is a common member of the salt marsh community and brackish backwaters along the Gulf and Atlantic coasts from Virginia to the west coast of the Yucatán Peninsula in Mexico. The species occurs inland along the Rio Grande Valley in Texas and as far as the State of Coahuila in northern Mexico. It is present along the coasts of the Bermuda Islands, but normally is absent from the West Indies. The species was collected once on Grand Bahama Island, *Allen 29* (GH), annotated by Britton & Millsaugh as *B. arborescens* (probably because the plant is neotonous), and was collected near Havana, Cuba, *Ekman 13,292* (F, CH, NY, US). The duplicates range from typical *B. frutescens* to more *B. cubana*-like and may represent part of a hybrid swarm. These collections by Eckman were originally identified as *B. cubana* and are from the type location of that taxon. Both the Cuban and Bahamian collections are probably only chance introductions. Figure 1 (dots) illustrates the distribution of the species based on herbarium collections.

MORPHOLOGICAL VARIATION

The species varies greatly in size of the heads and the degree of leaf serration-dentation. Field observations indicate that the variation in head size is in part due to environmental factors. The time of year when the head is produced and the general vigor of the plant affect head size. Various degrees of leaf serration-dentation occur throughout the range, although extreme forms are more common in southern Texas. Typically the blade margins are serrate along the basal third to half, while some specimens have some leaves with most of the blade serrate: Flamingo, Florida, *Godfrey et al. 63379* (FSU); Nuevo Laredo, Nuevo León, Mexico, *Frey & Frey 2337* (GH). While isolated individuals may appear to warrant taxonomic status, such extremes merely represent the ends of continuous variation of several characters in a single phenotype.

On some specimens the outer two involucral bracts may be large (1–2 cm) and appear more leaflike due to the lack of the long woody spine. The extreme forms of this variation are again merely the end of a continuum and do not warrant taxonomic recognition.

Field studies revealed that some plants may rarely produce leaves that are glabrate in part or entirely. This may represent some environmentally induced return to the seedling leaf form. Experimentally grown plants were found to produce several pairs of juvenile leaves that were glabrate and without serrate-dentate margins before producing more typical leaves. In this condition the seedlings may be confused with *B. arborescens*, although the involucral bracts that are produced by such unusually early flowering plants are typical. Figure 2 illustrates the branching pattern, leaves, involucre and phyllaries, and a disc fruit of *B. frutescens*.

BERMUDA. Castle Harbor, Admiral's Cove, *Brown & Britton 968* (NY). Long Bird Is., *Marble 762* (NY). St. David's Is., Red Bay, *Brown & Britton 1063* (NY). Walsingham, *Brown & Britton 281* (F, GH, NY, US); *Collins 305* (F, NY, US); *Rankin s.n.* (NY); *Marsh 1636* (F, GH, SMU, TEX).

MEXICO. CAMPECHE: S of Lerma, *Sauer 2429* (F). YUCATÁN: Progresso, *Gaumer 1161*

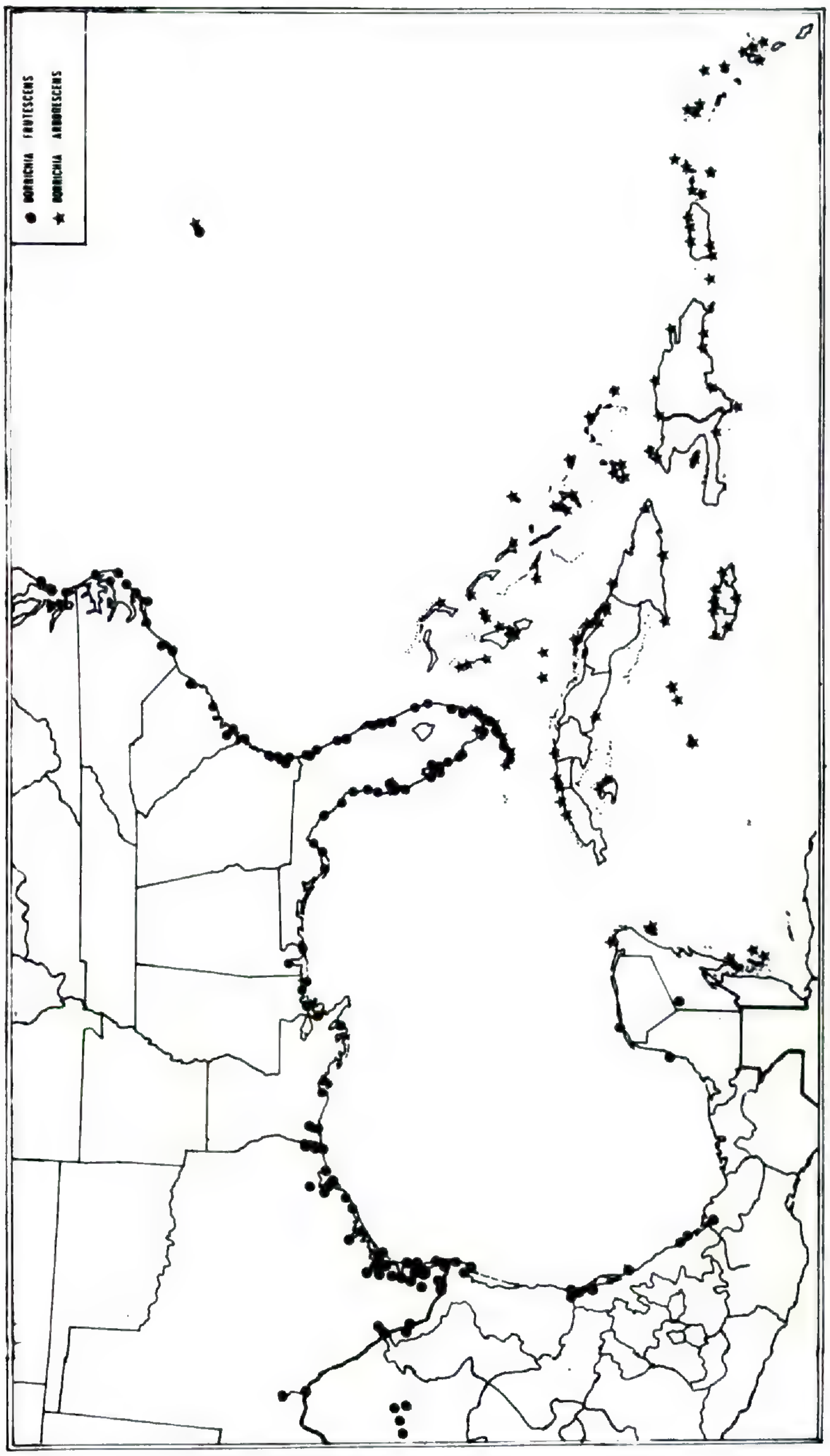

FIGURE 1. The distribution of *Borrichia frutescens* (dots) and *B. arborescens* (stars) based on herbarium collections. *Borrichia* × *cubana* (not shown) occurs in the Florida keys and was collected in 1917 and 1921 at the type locality west of Havana, Cuba.

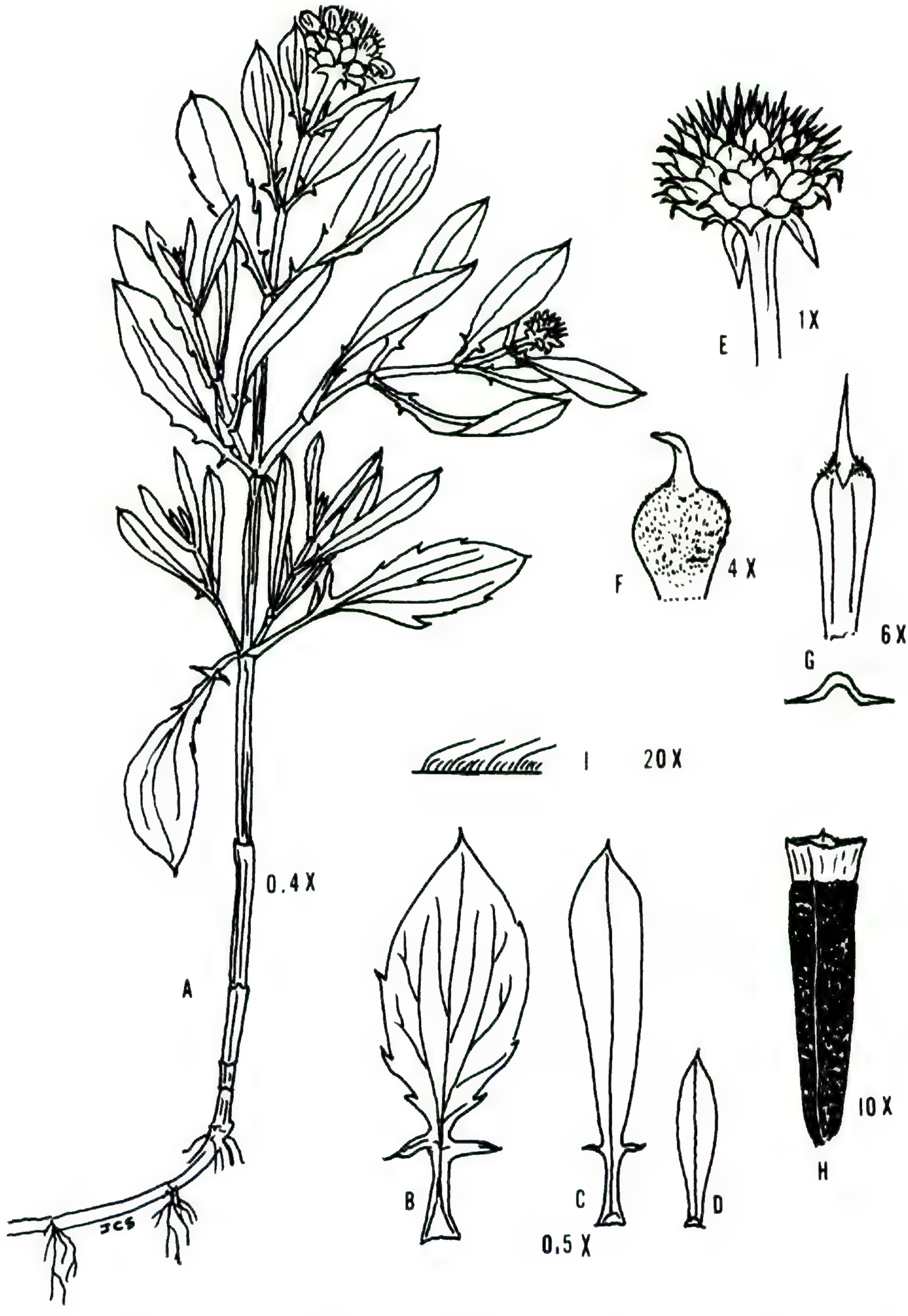

FIGURE 2. *Borrichia frutescens* (L.) DC.—A. Shoot from rhizome.—B–D. Primary stem leaf, branch leaf, higher level branch leaf, respectively (pubescence not indicated; all at same scale).—E. Fruiting head.—F. Phyllary of middle series.—G. Receptacle chaff.—H. Mature fruit of central disc floret.—I. Leaf surface pubescence diagram. (Based on many collections.)

(F, MO, US); *Lundell 7951* (F, GH, NY, TEX, US). COAHUILA: W of Hermanas, *Turner 6350* (TEX). Cuatro Ciénegas, *Marsh 2033* (F, GH, TEX). QUINTANA ROO: Lake Chichankanab, *Gaumer 2209* (F, GH, MO, US). SAN LUIS POTOSÍ: Haciende de Angosturo, *Pringle 3757* (F, GH, MO, US). TAMAULIPAS: S of Matamoros, *Wooten 29* (US). Tampico, *Palmer 100* (F, GH, MO, NY, US). VERACRUZ: Barra de Tuxpan, *Sauer & Gade 2985* (F). 4 km S of state line, *Newling & Gómez-Pompa 388* (GH). 8 km before Tampico. *Chiang 73* (F, GH).

UNITED STATES. ALABAMA: Mobile, Dauphine Is., *Mohr s.n.* (US). FLORIDA: Brevard Co., Titusville, *Nash 2289* (F, GH, MO, NY, US). Broward Co., Hollywood, *Demaree 18714* (FLAS). Collier Co., Marco, *Hitchcock s.n.* (F); *Standley 12793* (US). Citrus Co., Pirates Cove, *Genelle & Fleming 1272* (USF). Dade Co., Coconut Grove, *Young 50* (US). Elliot's Key, *Small & Nash s.n.* (NY). Homestead, *Godfrey 58125* (USF). Miami, *Garber s.n.* (GH, NY); *Small 5456* (GH, NY, US); *Small & Carter 1214* (F, NY). Duval Co., Shell Is., *Curtiss 1413* (F, MO, US). Franklin, NE of Alligator Pt., *Kral 2798* (FLAS, GH, NY, USF). Hernando Co., Pine Is. causeway, *Kral 7015* (FLAS, GH, USF). Hillsborough Co., Mullet Key, *Long 1264* (USF). NW Tampa, *Lakela 25012* (GH). Indian River Co., Vera Beach, *Demaree 41973* (SMU). Lee Co., Punta Rassa, *Hitchcock 136* (F, GH, MO, NY, US). *Standley 265* (F, GH, MO, US). Monroe Co., Big Pine Key, *Killip 41804* (F, US); *Traverse 715* (GH, SMU, TEX). Flamingo, *Traverse 624* (SMU, TEX). Pasco Co., Port Richey Bay, *Lakela & Patman 9983* (FLAS, GH, USF). Wakulla Co., Panacea Shores, *Henderson 63-1241* (TEX). GEORGIA: Glynn Co., Brunswick, *Small s.n.* (F, NY). St. Simon's Is., *Cronquist 5351* (GH, MO, NY, SMU). McIntoch Co., Sapelo Is., *Duncan 20162* (GH, SMU, TEX, UC). LOUISIANA: Cameron Pa., Cameron, *Tracy 8664* (F, GH, MO, NY, US). MISSISSIPPI: Harrison Co., Biloxi, Ship Is., *Demaree 31909* (F, TEX), *35023* (USF). Jackson Co., Horn Is. Wildlife Refuge, *Valentine s.n.* (FLAS, SMU). NORTH CAROLINA: Carteret Co., Beaufort, *Godfrey 6492* (US); *leClair 5863* (NY); *Channell & Rock s.n.* (GH). Hyde Co., Ocracoke Is., *Kearney 2285* (US). SOUTH CAROLINA: Charleston Co., McClellanville, *Godfrey & Tryon 251* (F, GH, MO, NY, US). Horry Co., Lillte R. Bindge, *Bell 7711* (USF). TEXAS: Calhoun Co., Port. Alto, *Drushel s.n.* (MO). Cameron Co., Boca Chica, *Webster & Wilbur 3042* (SMU). Galveston Co., E of Alvin, $n = 14_{II}$ *Raven & Gregory 19413* (TEX). Karnes Co., S of Kenedy, *Johnson 960* (SMU). Kenedy Co., El Toro Is., *Tharp 49128* (US). Nueces Co., Corpus Christi, *Heller 1786* (GH, MO, NY, SMU, US). San Patricio Co., Aransas Pass, *Schulz 834* (US). Sinton, *Wolcott & Barkley 16-413* (GH, NY, TEX). Webb Co., E of Laredo, *Gutierrez 88* (SMU, TEX). Banks of the Pecos, *Wright 1407* (GH, MO, NY, US). VIRGINIA: Accomac Co., Chincoteague Is., *Eiten 936* (NY). Anne Northhampton Co., Capeville, *Hunnewell 17007* (GH). Princess Anne Co., Lynnhaven Inlet, *Randolph 429* (GH).

WEST INDIES. BAHAMAS: Grand Bahama Is., *Allen 29* (GH).

2. **Borrichia arborescens** (L.) DC., Prodr. 5: 489. 1836.

Buphthalmum arborescens L., Syst. Nat., ed. 10. 1227. 1759. Based on Plumier, Pl. Amer. *tab. 106, fig. 2.* 1756.

Diomedea indentata Cass., Bull. Sci. Soc. Philom. Paris. 1817: 70. 1817.

D. glabrata H.B.K., Nov. Gen. Sp. Pl. 4: 213. 1820. TYPE: Cuba (not seen). Cites *Buphthalmum arborescens* L.

D. argentea H.B.K., Nov. Gen. Sp. Pl. 4: 213. 1820. TYPE: Cuba (not seen). Cites *Buphthalmum Peruvianum* Lam. and *B. lineare* Willd. Sensu D.C. pro parte ex syn. *B. peruviana* and *B. lineare.*

Buphthalmum canum L'Her. ex Dun. in DC., Prodr. 5: 489. 1836, pro syn.

B. argentea (H.B.K.) DC., Prodr. 5: 489. 1836.

Borrichia glabrata Small, Fl. S.E. U.S. 1263. 1903. TYPE: Florida, *Curtiss 1412* (NY, holotype; F, GH, MO, NY, isotypes).

Fruticose perennials to 1.5 m tall, decumbent to ascending, forming clones by rooting or drooping stems and by rhizomes. *Leaves* succulent, opposite, oblanceolate-oblinear, very shortly petioled, the blade attenuate; juvenile leaves of seedlings glabrous, apically serrate; adult leaves entire, mucronate, 5–10(–15) cm long, becoming reduced in size on higher order branches. *Heads* solitary, ovate; peduncles 0.5–5 cm long; phyllaries 10–16, the outer in pairs, succulent, ovate-elliptic, obtuse or acute, glabrate or sericeous, 6–9 mm long, the inner

oblanceolate acute to rounded, glabrous, 6–9 mm long; receptacle slightly convex, the chaff similar to the inner phyllaries, oblanceolate-linear, acute to rounded apically; ray florets pistillate, fertile, yellow, 7–15; disc florets perfect, fertile, yellow, 20–50. *Fruits* (cypsela) black at maturity, 4-angled, traversely depressed obtrullate to rhombic in cross-section, 3.5–5 mm long, pappus a 4-angled united crown, straw colored; heads hemispheric at maturity, dark brown with the apices of the phyllaries and chaff often disintegrating, whole heads disintegrating after one or more seasons. Chromosome number: $n = 14_{II}$ (possibly aneuploid with $2n = 26$–30).

DISTRIBUTION AND HABITAT

Borrichia arborescens is common along the rocky coasts and sandy marshes and beaches of the Florida Keys, Bermuda, the West Indies from Jamaica and Guadeloupe northward, and the barrier islands of Belize and the east coast of the Yucatán Peninsula. The species's northern extension in the United States is Miami, Florida. Figure 1 (stars) shows the distribution of *Borrichia arborescens* based on herbarium collections. In frequently collected areas some symbols have been left out for clarity.

MORPHOLOGICAL VARIATION

Two forms typically occur throughout the range: sericeous individuals with obovate-oblanceolate to oblanceolate leaves and glabrate individuals with similar or more linear leaves. The shape of the leaf varies considerably, even on the same plant in some cases. In the Florida Keys the glabrous form is the only one present, while elsewhere both forms may occur. Field work in the Bahamas indicates that the pubescent form may be an ecotype more adapted to the rocky limestone coasts, while the glabrous form is more common in the mangrove swamp areas and brackish lagoons. This is not absolute though and both forms may occur in most habitats.

Small (1903) segregated the extremely large glabrate-leaved individuals as *B. glabrata*, but later reconsidered and treated the form merely as a variety. In the Bahamas many plants were found to possess both glabrate and pubescent leaves. *Borrichia argentea* was the name applied to the other end of the continuum; plants with small, obovate, pubescent leaves. Near George Town, Great Exuma, Bahamas, individuals were found with leaves of the *glabrata*-type and leaves of the *argentea*-type. The existence of such populations indicates the existence of a single variable species. I (Semple, 1970) found the same situation for *Conocarpus erectus* L. and noted the existence of the intermediate forms in *Borrichia arborescens*. Plants with both glabrous and pubescent leaves have been collected throughout most of the range of the species and such intermediates probably exist everywhere both pure forms do. On Jamaica the pubescent form is dominant and the glabrous form is nearly absent. Some small islands appear to have only one form. This may be due to chance introduction of just the one form, but environmental factors favoring one form may exist. The genetics of the conditions have not yet been studied. One plant grown from seed was observed to cycle between glabrate leaves produced in late winter and spring and pubescent leaves produced in the summer and fall. These observations

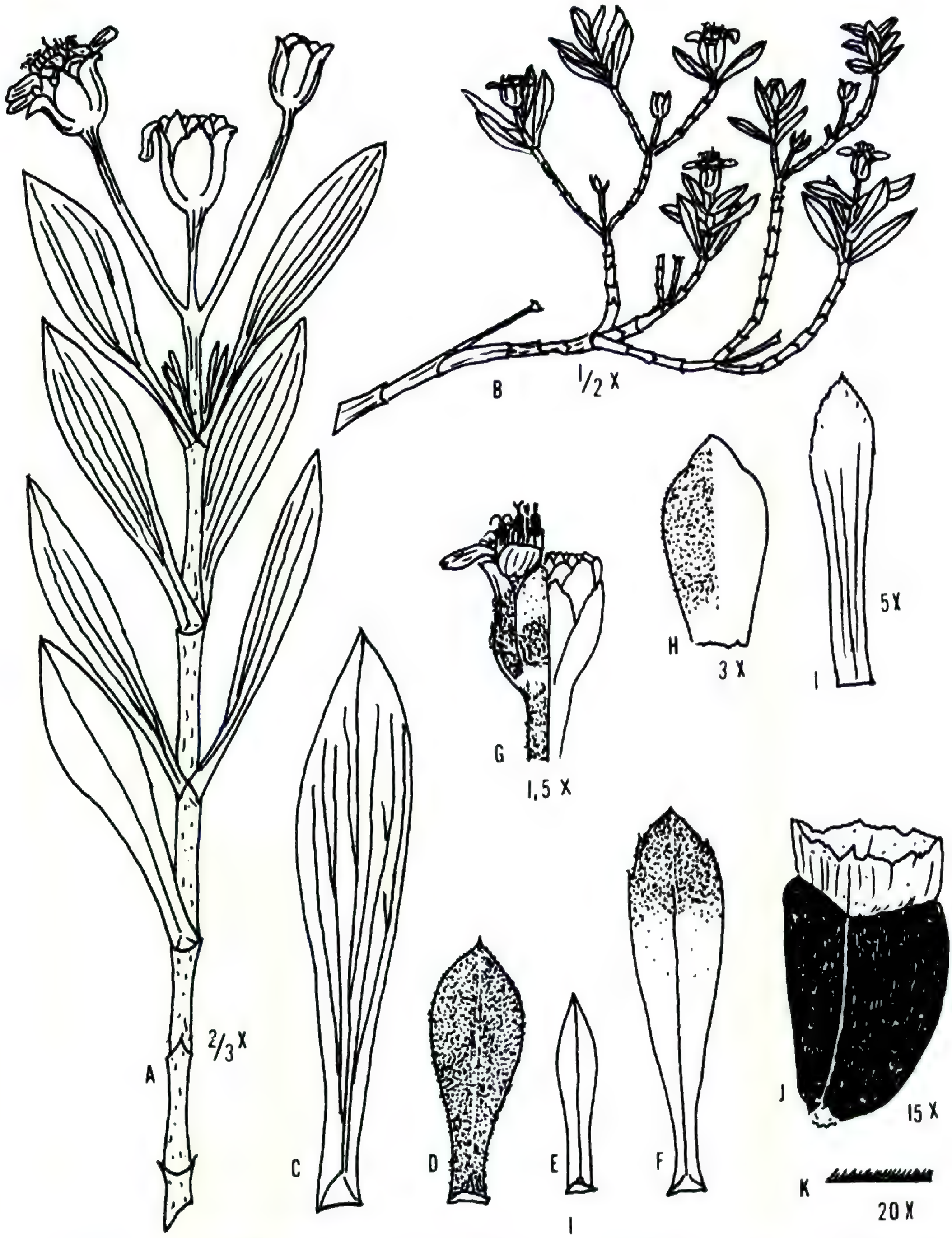

FIGURE 3. *Borrichia arborescens* (L.) DC.—A. Terminal portion of a young shoot. —B. Branch from an older procumbent plant.—C–F. Variation in leaf morphology (all the same scale).—C. Glabrous leaf of the *glabrata*-form.—D. Pubescent leaf of the *argentea*-form. —E. Glabrous leaf from an upper branch (pubescent leaves look similar).—F. Juvenile leaf of a plant that later produced pubescent leaves.—G. Head illustrated in flowering condition on the left side and fruiting condition on the right side.—H. Phyllary (one side illustrates location of pubescence when present).—I. Receptacle chaff.—J. Fruit of peripheral floret (central floret fruit similar to Fig. 2H).—K. Leaf surface diagram illustrating nature of pubescence when present on leaves.

were made while the plant was in a greenhouse in Canada, so conditions may be too different from the wild habitat for the observations to be of great significance. The observations do indicate that the nature of the indument can be changed by modification of the environment. Figure 3 illustrates the morphological characteristics of *B. arborescens*.

BELIZE Glover's Reef, Long Cay, *Fosberg & Sachet 53804* (GH, MO). Ambergris Cay on Barrier Reef, *Stoddart 445* (UH), *446* (IJ, US). Stamn Creek, *Shipp 575* (F, GH, MO, NY).

BERMUDA. Gibbit Is., *Collins 304* (F, GH, NY, US), *397* (GH). Hungry Bay, *Bailey et al. s.n.* (GH). Long Bud Is., *Brown 707* (GH, US, NY), *709* (GH, NY). Smith's Parish, Flatts Inlet, *Moore 2851* (F, GH, NY). Warwick, *Manuel 104* (GH); *Robinson 170, 171, 172* (all GH).

MEXICO. QUINTANA ROO: Tancah, *Steere 2529* (US). Holbox Is., *Gaumer s.n.* (US). Cozumel Is., *Gaumer 89* (NY).

UNITED STATES. FLORIDA: Dade Co., Coral Gables, King's Bay Country Club, *Morton* (BUS). Elliott's Key, Caesar's Rock, *Britton 370* (F, NY). *Small & Nash s.n.* (NY). Key Largo, Newport, *Eaton 429* (TEX). *Traverse 662* (GH, SMU, TEX). Miami, *Small & Wilson 1894* (NY). Sands Key, *Rodham s.n.* (GH). Monroe Co., Bahia Honda, *Simpson 365* (F, US). Big Pine Key, *Killip 41688* (F); *Killip & Swallen 49303* (US); *Seibert 1267* (GH, MO). Everglades Natl. Park, *Graighead s.n.* (GH). Grassy Key, *Stern 1482* (GH, US). Key West, *Lakela 27823* (GH); *Hitchcock s.n.* (F). Little Torch Key, *D'Arcy 3046* (FLAS). Lower Matecumbe Key, *O'Neill 7613* (GH, NY, US); *Weber s.n.* (FLAS). Marquesas Keys, *Lansing 2157* (F, NY). Ragged Keys, *Small & Carter 3120* (NY). Torch Key, *Curtiss 5436* (GH, MO, NY, US).

WEST INDIES. BAHAMAS: Abaco, Sandy Pt., *Proctor 30548* (IJ). Acklin's Is., *Brace 4397* (F, NY). Andros Is., Golden Cay, *Dawson 26895* (US). Andros Town, *Dawson 26622* (US). Bimini, NIS., *Howard 10018* (GH, NY, SMU, US). SIS., Port Royal, Rabbit Cay, *Gillis 11313, 11314* (both IJ). Caicos, Middle Is., *Burch 4293* (NY). Crooked Is., *Hitchcock s.n.* (MO). Eleuthera Is., the Current, *Lewis 7197* (MO, NY). Great Exuma, Jewfish Light Chain, Hummingbird Cay, *Nickerson & Kessler 2743* (GH). Grand Turk, East Bay, *Proctor 8771* (IJ); *Nash & Taylor 3886* (F, NY). Inagua, Sandy Pt., *Nash & Taylor 1390* (NY); *Dunbar 77* (GH). Mayaguana Is., Abraham Bay, *Wilson 7525* (F, GH, NY). New Providence Is., Nassau, *Wright 9, 25* (both F, GH, NY). Salt Key Bank, Anguilla, *Wilson 8075* (MO, NY), *8107* (F, NY). Watlings Is., *Wilson 7288* (F, GH, NY). CAYMAN ISLANDS: Grand Cayman, *Armour 1239* (F); *Brunt 1687, 1884* (both IJ), *268* (MO, NY); *Proctor 11989* (GH). Little Cayman, *Kings 40* (MO, NY). CUBA: Camaquey, Cayo Palo, *Shafer 2732* (F, NY, US). Cayo Paredon Grande, *Shafer 2759* (F, NY, US). Havana, Havana, *Curtiss 750* (F, GH, MO, NY, US). Playa de Marianas, *León 3713, 5024* (both NY). Isle of Pines, Bibijagua, *Jemmings 114* (GH, NY, US). Matanzas, *Britton & Shafer 44* (NY). Oriente, S of Cape Cruz, *León 16349* (NY). Santiago, *Clemente 5318* (NY). Pinar Del Río, Mariel, *Palmer & Riley 729* (US). Santa Clara, Cienfuegos, *Jack 8304* (US). Gavitán, *Howard 4962* (GH, NY). Santiago, Baracoa, *Pollard et al. 197* (F, GH, MO, NY, US). HAITI: Bayeux in Dept. du Nord, *Eleman 2556* (GH, IJ). Mahautiere, *Eyerdam 87* (F, GH, US). La Gonave Is., Bouchia Lagone, *Ekman 8688* (F, NY). Tortue Is., La Valle, *Leonard 11430* (GH, NY, US). *Holdridge 1417* (NY, US). JAMAICA: Bluefields Bay, *Harris 9975* (NY, US). Port Antonio, *Maxon & Killip 282* (US); *Millspaugh 985* (F); *Wight 160* (F, NY). Hanover, Esher Cove, *Proctor 23470* (IJ). Middlesex Co., Dry Harbour, *Hunnewell 11173* (GH). St. Ann's Hall, *Fosberg 42686* (US). St. Mary, Port Maria, *Proctor 7531* (IJ). Oracabessa, *Proctor 6648* (IJ, US). St. Thomas, Holland Bay, *Bengry s.n.* (FLAS, IJ, MO). Westmoreland, Homer's Cove, *Proctor 33070* (IJ). LESSER ANTILLES: Anquilla, Flat Cap Pt., *Proctor 17628* (IJ). Antiqua, Mamora Bay, *Box 1302* (US). Barbuda, *Cowan 1667* (GH, IJ, NY, US). Guadeloupe, Grande Terre, Moule, *Proctor 19960* (IJ, US). Marie Galante, Anse Piton, *Proctor 21096* (IJ, US). St. Croix, *Ricksecker 24* (F, GH, MO, NY, US). Virgin Is., Anegada Is., *D'Arcy 4806* (US). PUERTO RICO: Arecibo, *Sargent 771* (US, TEX). Guanica, *Velez 645* (NY). Salimas de Cabe, *Urban 535* (GH, US). San Juan, *Underwood & Griggs 916* (NY, US). Is. Culebra, *Britton & Wheeler 239* (NY, US). Mona Is., *Britton et al. 1765* (NY). Vieques Is., *Shafer 2671* (NY, US). SANTO DOMINGO: Barahona, Beata Is., *Howard 12422* (GH, US). Trujin, *Abbott 1681* (US). Ciudad Trujillo, *Allard 14386* (US). Puerta Plata, LaBoca Cliffs, *Ekman 14589* (GH, US); *Jiménez 4358A* (US). San Pedro de Macoris, *Rose et al. 4263* (NY, US). Samana Penisula, Cape Samana, *Abbott 1188a* (US).

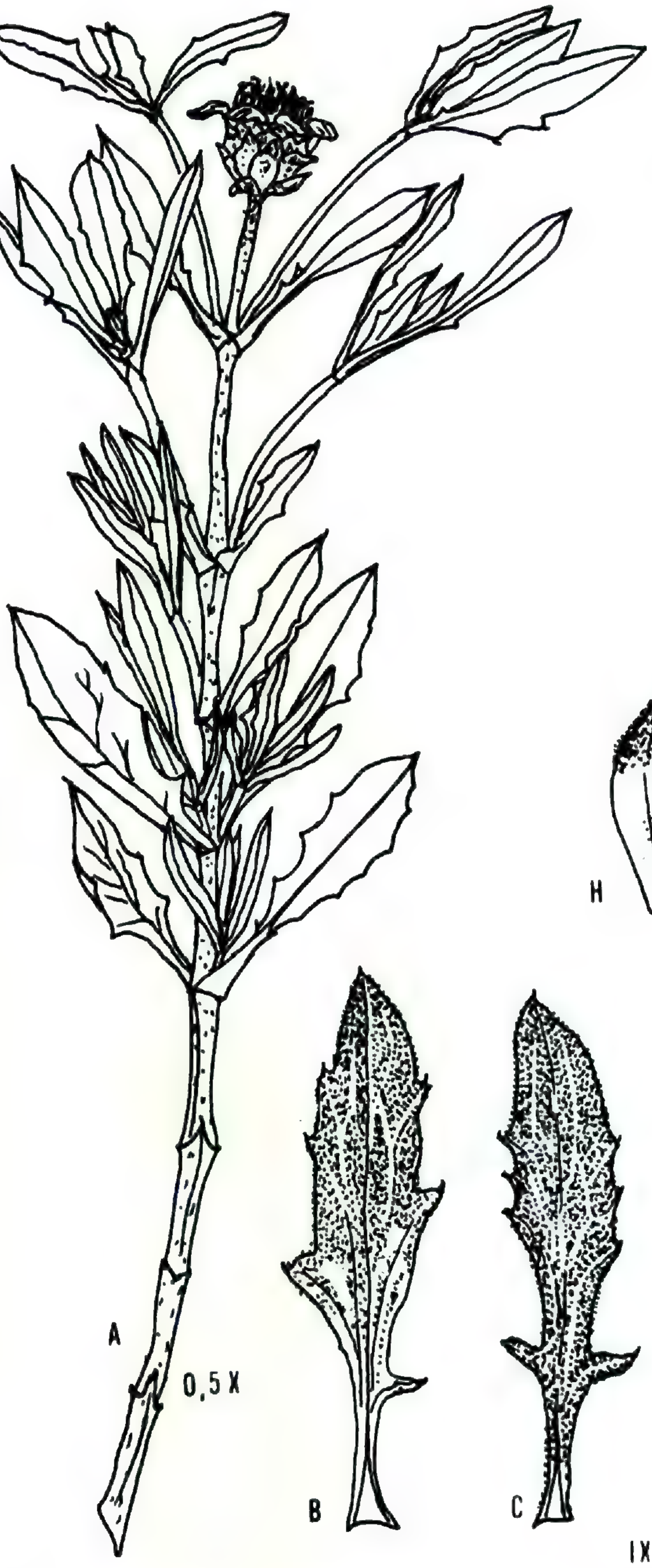

FIGURE 4. *Borrichia* × *cubana* Britton & Blake.—A. Branch.—B–F. Range in leaf morphology present on same plant.—B–C. Leaves occurring on primary and secondary stems and branches.—D. Leaf occurring on secondary and higher level branches.—E–F. Leaves occurring on higher level branches.—G. Head illustrated in flowering condition on the left side and fruiting condition on the right side.—H. Phyllary of middle series.—I. Receptacle chaff.—J. Leaf surface diagram illustrating nature of pubescence when present on leaves.

3. **Borrichia × cubana** Britton & Blake (pro sp.) stat. nov., Mem. Torrey Bot. Club 16: 116. 1920. TYPE: Cuba, Havana, swamp near Atares Castle, June 1917, *León 7244* (NY, annotated as the holotype by E. K. Schofield, 1973; NY, annotated as isotype by E. K. Schofield, 1973).

Fruticose perennials. Leaves opposite, heteroblastic; primary stem leaves elliptic petiolate, serrate-spinulose along the mid portion of the blade, undulate and coriaceous, more succulent with age; upper branch leaves reduced, sessile, oblanceolate-linear, glabrate to long puberulent. *Heads* solitary, hemispherical; phyllaries 16–25, in several subequal series, 5–8 mm long, ovate with cuspidate tips, pubescence similar to that of the leaves; chaff slightly folded, oblanceolate cuspidate, but not spinulose, equal to the bracts in length; ray florets pistillate, apparently fertile, yellow, 14–25; disc florets perfect, apparently fertile, yellow, 25–60. *Fruit* (cypsela) black at maturity, 4-angled, traversely depressed obtrullate to rhombic in cross-section, 3–5 mm long; head brown to black at maturity, hemispheric; phyllaries not thickening with age. Chromosome number: $n = 14_{II}$; Semple (1978) described meiosis in the hybrids.

Detailed experimental and field observations that support the status change of this taxon from that of species to a hybrid between *B. frutescens* and *B. arborescens* were given by Semple & Semple (1978). In the protologue Britton noted that he thought that *B.* × *cubana* was closely related to *B. frutescens*. The plants are intermediate in nearly all characters between the two parental species. The bracts are large like *B. arborescens* and cuspidate, which is intermediate between the acute *arborescens* condition and the spinulose *frutescens* condition. The hybrids are common in the Florida Keys, the only area where the two parent species are normally sympatric. No hybrids have yet been collected from Bermuda, but they may be present since both parents occur there. There appears to be, or has been, only one population of hybrids in Cuba—namely, the type locality from which several collections were made in 1917 and 1921 (*León 6870*, *7244* and *Ekman 13292*, respectively). The latter is a mixed collection of specimens appearing to be *B.* × *cubana* and some *B. frutescens* and may represent a sample of a hybrid swarm. It is possible that Ekman sampled the actual parent involved in the cross, but this can not be proven.

Experimental crosses were made between *B. frutescens* and *B. arborescens*. The F_1 progeny were morphologically similar to cuttings of *B.* × *cubana* collected in Florida. Figure 4 illustrates the intermediate morphological condition of *B.* × *cubana*.

CUBA. HAVANA: Castillo de Etares, *Ekman 13292a* (GH, NY, MO, US); *León 6870* (NY).

UNITED STATES. FLORIDA: Dade Co., Adams Key, *Small & Mosier 5736* (USF). Coral Gables, King's Bay Country Club, *Semple 1698* (MO, US, WAT). S of Elliott's Key, Caesar's Rock, *Britton 369* (F, NY). E of Gould, Black Point, *Semple 1709* (CAN, MO, WAT, US). Miami, MacArthur Causeway, *Semple 1703* (MO, US). Sands Key, *Semple 1700-6* (MO, US). Monroe Co., Big Pine Key, *Cornman 2111* (MO); *Seibert 1270* (GH, MO); *Semple 1737* (MO, US, WAT). Craig Key, *Semple 1755* (MO, US). Key West, *Small & Small 4911* (GH, US). Long Key, *Long et al. 2249* (USF). Lower Matecumbe Key, *Semple 1719* (MO, US). Marquesas Group, Man Key, *Lansing 2360* (F, NY). Woman Key, *Lansing 2420* (F). Saddle Bunch Keys, *Semple 1734* (MO, US).

4. **Borrichia peruviana** DC., Prodr. 5: 489. 1836. TYPE: see following discussion.

Buphthalmum peruvianum Lam., Encyl. Méth. 1: 515. 1785.
B. lineare Willd., Sp. Pl. 3: 2230. 1803. New name for *B. peruvianum* Lam.

This taxon is known only from the type collection, which is without flowering or fruiting heads. De Candolle (1836) apparently recognized it as a species because some of the leaves have a few spinulose teeth along the mid portion of the blade. These leaves are unlike the other specimens in the other taxa that De Candolle had for examination (as seen on microfiche). The specimen was collected by Dombey in "Peru," far out of the range of the other species, if it actually came from that country. The collection may represent an aberrant *B. frutescens* introduced to "Peru," where the species did not establish itself. A second possibility is that the specimen is from a locale where *B.* × *cubana* occurred and the specimen is either a hybrid or back-cross. Such a speculative conclusion is based on the presence of similar leaf margin serrations on hybrid plants. If the type of *B. peruviana* is in fact a hybrid between the only true species in the genus, than the name would have priority over *B.* × *cubana*. Until the original material can be aligned with certainty with one of the taxa treated in this paper, the name *B. peruviana* cannot supplement any of the names used here.

EXCLUDED SPECIES

Borrichia demissa DC., Prodr. 5: 489. 1836.

Examination of the type material by Dr. M. Dittrich of Geneva at my request indicates that the pappus of this plant consists of 6–8 subulate scales. For this reason the species is excluded from the genus *Borrichia* as treated here.

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DYSTOVOMITA, A NEW GENUS OF NEOTROPICAL GUTTIFERAE[1]

W. G. D'Arcy[2]

Abstract

Because of its distinctive placentation, axillary structures, and unusual inflorescence structure, Engler's *Tovomita* sect. *Dysovomita* is raised to generic level. The new genus now consists of three species [*D. brasiliensis* D'Arcy, *D. clusiifolia* (Maguire) D'Arcy, *D. pittieri* (Engler) D'Arcy], the first newly described.

Dystovomita (Engler) D'Arcy, gen. nov.

Tovomita sect. II *Dystovomita* Engler, Bot. Jahrb. Syst. 58, Beibl. 130: 8. 1923. TYPE: *Tovomita pittieri* Engler = *Dystovomita pittieri* (Engler) D'Arcy.

Glabrous dioecious *trees*. *Leaves* opposite, entire, the costa prominent, the lateral veins slightly arcuate, evenly spaced, the minor venation inconspicuous; petioles stout; axillary structures drying hard, dark, conspicuous. *Inflorescences* lateral on the stems or terminal, sessile, fascicled, cymose panicles; minute bracts and bracteoles present. *Flower* buds globose or ovoid; sepals 2–4, the outer pair sometimes reduced to minute appressed scales (?bracts), the inner pair imbricate or fused in bud, opposite, decussate; petals 4, imbricate and overtopping the bud; stamens numerous, the filaments free or appearing as if in fascicles, the anthers terminal, 2-lobed along the sides of the filament apex, 4-loculed; ovary 3–5-locular, the styles short or wanting, reflexed over the ovary, the stigmas ligulate or spatulate, adaxial and hence facing outwards from the ovary, the ovules 1–2 per locule, pendant, axile, the funiculus affixed to the upper ¾ of the placental column, the second ovule when present partly superposed. *Fruit* a small apically dehiscent berry, the outer bracts persistent but the other perianth parts deciduous; seeds faboid, striate, exarillate with a convex, discoid, hard caruncle.

a. Flower buds ovoid with a sharp point; inflorescences arising on slender twigs; Brazilian species ..... 1. *D. brasiliensis*
aa. Flower buds globose, blunt topped; inflorescences arising on stout branches or twigs; Venezuelan or Central American species.
  b. Outermost perianth consisting of 2 sepals (bracts) less than ¼ as long as the bud; pedicels mostly lacking bracteoles; Venezuelan species ..... 2. *D. clusiifolia*
  bb. Outermost perianth consisting of 2 sepals nearly as long as the bud; pedicels mostly with 2 bracteoles on the lower half; Central American species .... 3. *D. pittieri*

1. **Dystovomita brasiliensis** D'Arcy, sp. nov.

Arbor, foliis ellipticis vel ovatis coriaceis; alabastris ovoideis, e bracteolis oblongis deciduis emergentibus.

Tree 15 m tall; trunk 15 cm in diam.; twigs slender, subterete or compressed, drying smooth but minutely sulcate, reddish brown. *Leaves* coriaceous, broadly

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[1] Assisted by National Science Foundation Grant DEB 72-02441 A05.
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Ann. Missouri Bot. Gard. 65: 694–697. 1978.

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elliptical or obovate, ca. 15 cm long, 8 cm wide, the costa prominent, raised rounded beneath, the lateral veins ca. 10 on each side, arcuate at the margin but not forming a submarginal vein, not loop connected, obscure above, prominent beneath, the minor venation of weak but continuous intermediate lateral veins especially upwards, and strongly ascending secondary lateral veins pinnate from many of the main lateral veins, drying discolorous, slatey above, reddish beneath; petioles 2–3 cm long; pseudostipules widely spreading, 5–6 mm long. *Inflorescences* lateral on the twigs or terminal, fascicles of short, somewhat congested cymose panicles, sometimes umbellate, to 7 cm tall; peduncles sharply compressed; pedicels sharply compressed, ca. 8 mm long. *Flower* buds ovoid, emerging from oblong, costate, deciduous, completely fused bracteoles ca. 2 mm long, minutely ciliolate, the sepals completely fused in bud, the tips coming to a sharp point.

TYPE: BRAZIL. AMAZONAS, Mun. São Paulo de Olivenca, basin of creek Belem, tree 50 ft high, trunk 6 inches in diam., tierra firma, high forest, *Krukoff 8714* (MO, holotype).

This species is known only from the type collection which is in bud. The leaf shape, pseudostipules, inflorescence, and appearance of the bud identify this as a member of *Dystovomita*.

2. **Dystovomita clusiifolia** (Maguire) D'Arcy, comb. nov.

Chrysochlamys clusiaefolia Maguire, Bol. Soc. Venez. Ci. Nat. 25: 225, *pl. 1*. 1964. TYPE: Venezuela, *Steyermark & Farinas 90941* (NY, holotype not seen; VEN, isotype).

VENEZUELA. FEDERAL DISTRICT: between Limón and Colonia Tovar, 1500 m, *Steyermark & Maguire 60030* (US), *60031* (MO). FALCÓN: Montaña de Paraguariba 5 km al Este del Hotel Parador, Sierra de San Luis, 1300 m, *Steyermark 99314* (US).

3. **Dystovomita pittieri** (Engler) D'Arcy, comb. nov.—FIG. 1.

Tovomita pittieri Engler, Bot. Jahrb. Syst. 58, Beibl. 130: 8. 1923. TYPE: Costa Rica, *Pittier 16094* (B, not seen; US, isotype).

Chrysochlamys clusiaefolia subsp. *panamaensis* Maguire, Phytologia 36: 395. 1977. TYPE: Panama, *Gentry & Mori 13769* (MO).

The two Colombian collections cited below are in fruit; they may be specifically distinct from *D. pittieri*.

COSTA RICA. Montagne de Tuis, 1000 m, *Pittier 16094* (US). Cloud forest above Wilson's finca 6 km S of San Vito de Java, 5000 ft, *Raven 21791* (MO).

PANAMA. Cerro Mali base camp, Colombian border, 1400 m, *Gentry & Mori 13769* (MO). Elfin forest, Cerro Caracoral, 1000 m, *Duke & Dwyer 15102* (MO).

COLOMBIA. Hills behind logging camp below first rapids on Río Truando, 40–200 m, *Duke 13320* (MO). Top of Serrania del Darién E of Unguia, 1400 m, *Gentry et al. 16775* (MO).

The difficulties of separating the clusioid genera *Tovomita*, *Tovomitopsis*, and *Chrysochlamys* have been alluded to by Maguire (1964, 1977) and others, and the solution taken by Standley & Williams (1961) to combine them all may be correct. These genera are close relatives of *Clusia*, but they have few ovules, only 1 or 2 in each of the 3–6 locules. The venation patterns differ somewhat as well, for there is a strong costa and distinct, evenly spaced pinnate venation on each side of it. In *Clusia* the ovules are mostly numerous, and the venation pattern

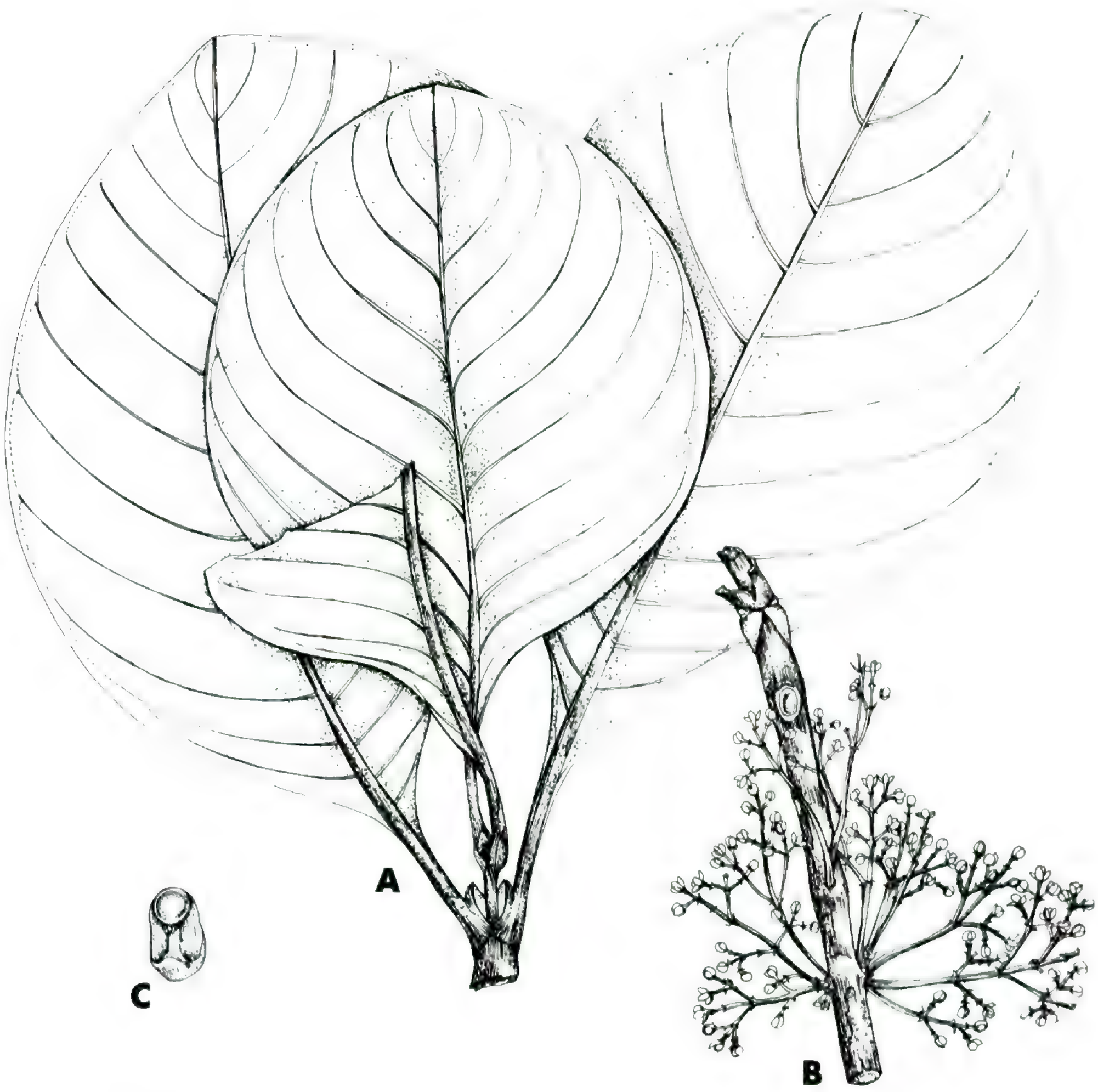

FIGURE 1. *Dystovomita pittieri* (Engler) D'Arcy—A. Habit. Note conspicuous axillary structures (× ½).—B. Inflorescence (× ½). [After *Gentry & Mori 13769* (MO).]—C. Seed. Note discoid caruncle (× 4). [After *Duke & Dwyer 15102* (MO).]

tends to be of strongly ascending, closely spaced veins from a costa which is conspicuously attenuate towards the apex. The three genera noted above have been separated on characters of the seed aril or arilloid and on the prefloration of the bud. In addition, *Chrysochlamys* is supposedly distinct in having 5-merous flowers, while *Tovomita* has 2- or 4-merous flowers. In all published information I have seen and in the ovaries I have opened, these genera have ovules which are basifixed and ascending or medifixed. Maguire (1977) characterized *Chrysochlamys* as having a cauliflorous inflorescence, but this appears to be a variable character; the original illustration of the type species, *C. multiflora* Poeppl. & Endl. shows a terminal inflorescence, and in the material I have seen labeled *Chrysochlamys*, inflorescences are only sometimes lateral on young twigs, not appearing to arise from stems of some maturity as the term cauliflorous usually connotes.

In the species of *Dystovomita* the venation patterns are like those in *Tomovita*, *Tovomitopsis*, and *Chrysochlamys*, and there are only 1 or 2 ovules per locule. However the ovules are pendant, affixed high on the abaxial side, and the testa has lines of tubercules, not veins, which are longitudinally oriented without respect to the hilum. In the case of two of the species, the inflorescence is cauliflorous on mature wood. The fruit is a globose, ellipsoid, or ovoid berry much smaller than is usual in the other genera, and within it there is no sign of an aril. The seeds are longitudinally lined by minute raised dots, and the discoid caruncle is hard, not at all fleshy.

Interpretation of the perianth presents some difficulty. In *Dystovomita pittieri* the pedicel bears two minute bracteoles on the lower half, much as in many species of *Tovomita*, but in *D. clusiifolia* these are borne at the base of the flower. Because I believe these bracts to be homologous with the outer sepals of many species of *Tovomita*, I refer to them as sepals. It is not surprising then that the two species have different numbers of sepals, *D. pittieri* having 2 sepals and 4 petals plus a pair of bracteoles low on the pedicels, and *D. clusiifolia* having 4 sepals and 4 petals but no bracteoles on the lower pedicel. But in each case, the petals are enclosed apically by only one pair of sepals, a situation rare in *Tomovita*, *Tovomitopsis*, and *Chrysochlamys*. In *D. brasiliense* there are deciduous bracteoles, and the outer sepals are completely fused, as in many species of *Tovomita*.

One conspicuous feature of dried specimens of *Dystovomita* is the lignified, stout, axillary structures which appear in each axil and which can also be seen at the apices of the stems between the last-emerged leaves. Similar structures are reported in other genera of Guttiferae but not in the *Tovomita* group of genera. The morphological identification of these structures is uncertain; they may be stipules (rare in the family), axillary buds, or enations of the petiole.

Field notes indicate that members of this genus lack the stilt roots common in other species of the *Tovomita* group, and that there is little or no milky sap, also a common characteristic of the Guttiferae.

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A PRELIMINARY SYNOPSIS OF *SALPIGLOSSIS* AND OTHER CESTREAE (SOLANACEAE)[1,2]

W. G. D'Arcy[3]

Abstract

The genera *Browallia, Cestrum, Hunzikeria, Leptoglossis, Nicotiana, Nierembergia, Petunia, Reyesia,* and *Salpiglossis,* all members of the mainly Neotropical tribe Cestreae of the Solanaceae, are reviewed and generic lines are discussed. *Hunzikeria, Leptoglossis, Reyesia,* and *Salpiglossis* are given extensive attention, and a new species of *Hunzikeria* is described. *Bouchetia* is placed into synonymy under *Salpiglossis.* An evolutionary path from primitive ancestors to modern, advanced members of the group is postulated.

Several genera of Solanaceae in tribe Cestreae have long been subject to confusion, and this paper suggests resolution of some of the problems. The names *Bouchetia, Browallia, Cestrum, Hunzikeria, Leptoglossis, Nicotiana, Nierembergia, Petunia, Reyesia,* and *Salpiglossis* are reviewed. The plants are mostly herbs or diminutive shrubs, and they occur in North and South America, some genera being disjunct. Although the study has spanned five years, this paper must be regarded as a report of unconcluded work rather than a completed investigation. Few living plants were seen and the herbarium survey was not exhaustive. In particular, species limits require definition. As the early emphasis was on North American species, these species receive more detailed treatment than those of South America.

Classification and Origins

Wettstein (1892, 1895) placed the genera discussed here into two tribes, the Cestreae and Salpiglossideae, separating the Salpiglossideae by their reduced number of stamens. Within the Cestreae, he recognized three subtribes: the Cestrinae with *Cestrum* and two discordant genera; the Goetzeinae, which is not solanaceous, and the Nicotianinae with *Nicotiana* and several of the genera discussed here. D'Arcy (in press) placed both tribes in subfamily Cestroideae. In the belief that *Cestrum, Nicotiana,* and *Salpiglossis* represent different levels of evolution within the same phylad and should not be separated into different tribes, Wettstein's subtribe Nicotianinae and tribe Salpiglossideae are here united into one tribe, Cestreae. Hunziker (1977) proposed the tribes Schwenkieae and Parabouchetieae for elements in subfamily Cestroideae which are distant from the pre-*Cestrum* ancestor of tribe Cestreae. Evidence has mounted (Gentry, in press) that the Australian elements of subfamily Cestroideae other than *Nicotiana* also have origins remote from the *Cestrum* ancestor and should be separated as tribe Anthocerceae. With separation of these three tribes, most of the other genera of subfamily Cestroideae appear to form a natural unit, the tribe Cestreae, with

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[1] Assisted by National Science Foundation Grant DEB 72-02441-A05.
[2] A review of this paper by Johnnie L. Gentry is gratefully acknowledged.
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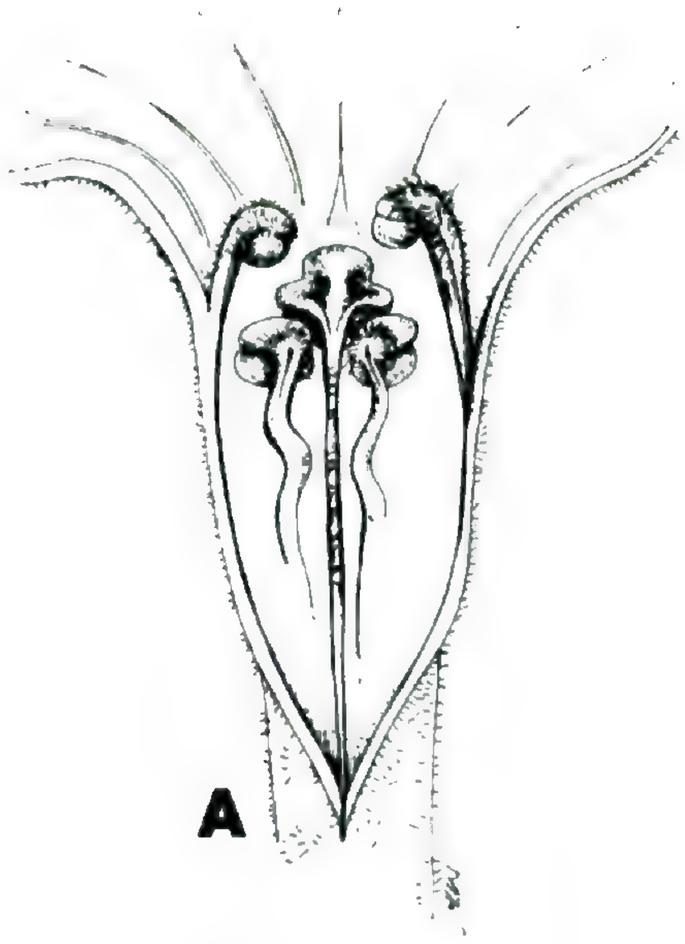
Ann. Missouri Bot. Gard. 65: 698–724. 1978.
0026-6493/78/0698–0724/$02.75/0

the following genera: *Benthamiella*, *Browallia*, *Brunfelsia*, *Cestrum*, *Combera*, *Fabiana*, *Hunzikeria*, *Leptoglossis*, *Nicotiana*, *Nierembergia*, *Phrodus*, *Petunia*, *Reyesia*, *Salpiglossis*, *Sessea*, and *Streptosolen*. Some genera of subfamily Cestroideae are of uncertain placement, e.g., *Sclerophylax* (see Hunziker, 1977) and *Salpiglossis* (see Tucker, 1969).

Floral Evolution

While there may be several explanations for the variation in floral morphology in genera of the group, D'Arcy (1975) suggested one explanation which he believed to be based on selective pressures by pollinators. This explanation postulated that starting with a campanulate corolla with stamens inserted low in the corolla tube and clustered loosely at the mouth as in *Petunia* or *Nicotiana* subgenus *Rustica*, there has been a tendency towards closure of the corolla mouth with compression of the anthers and stigma, and in some genera such as *Browallia* (Fig. 1A) or *Hunzikeria* (Fig. 1B), the corolla mouth is tightly plugged by stamens or stigma. Concurrent with this change in floral form have been tendencies for higher insertion of stamens, fusion of filaments, reduction of anthers, and elaboration of style. At this stage the stamens are didynamous and the corolla is irregular. Following this intermediate stage of small-mouthed corollas, further evolution appears to have taken place in two genera, *Nierembergia* and *Salpiglossis*. In *Nierembergia* (Fig. 1F), the anthers and stigma have become exserted from a narrow corolla mouth. The connation of filaments may have evolved before this exsertion. In *Salpiglossis* (Fig. 1E), the corolla seems to have opened again, taking on a shape much like that of the unspecialized *Petunia*, with reduced stamen number and anther thecae, and a somewhat elaborated stigma remaining as evidence of earlier passage through the intermediate form just noted. Whether or not the genera are undergoing the exact evolutionary steps just outlined, it is plausible to classify the genera into several groups according to level of floral specialization (Table 1).

The above proposal can be examined in the light of trends within natural and extant genera. Within *Cestrum* (D'Arcy, 1973, 1975) there is a trend from the wide corollas and low stamen insertion of sect. *Habrothamnus* to narrow corollas with higher insertion in sect. *Cestrum*. In *Nicotiana* (Goodspeed, 1954) species in the more primitive subgenus *Rustica* have low stamen insertion and anthers and stigma loosely clustered at the corolla mouth, while in the more advanced subgenus *Petunioides* many species have high stamen insertion and the anthers and stigma are compressed at the mouth of salverform corollas. However, in members of subgenus *Nicotiana* (*Tabacum*), which is also a specialized group according to Goodspeed, stamen insertion has remained low while the stamens and style are long exserted from an open, asymmetrical corolla mouth; this flower corresponds in some ways to Stage III noted in Table 1, but it is uncertain whether this flower ever underwent an evolutionary Stage II. Thus within *Cestrum* and *Nicotiana* we can see trends corresponding to the three stages proposed above, but in subgenus *Nicotiana* current morphology suggests some different course of evolution. The pre-Cestroid ancestor postulated by Goodspeed may well have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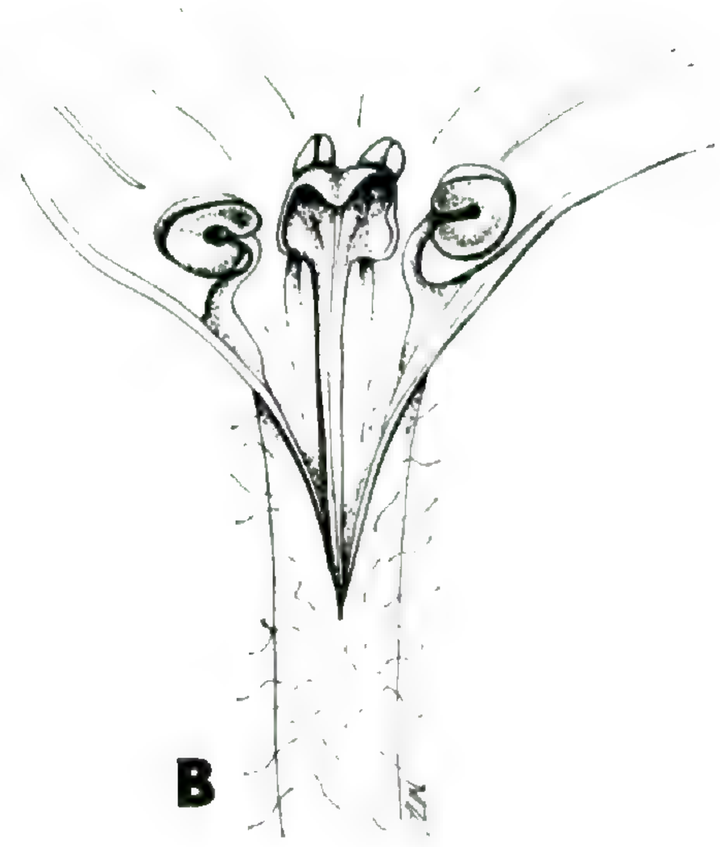
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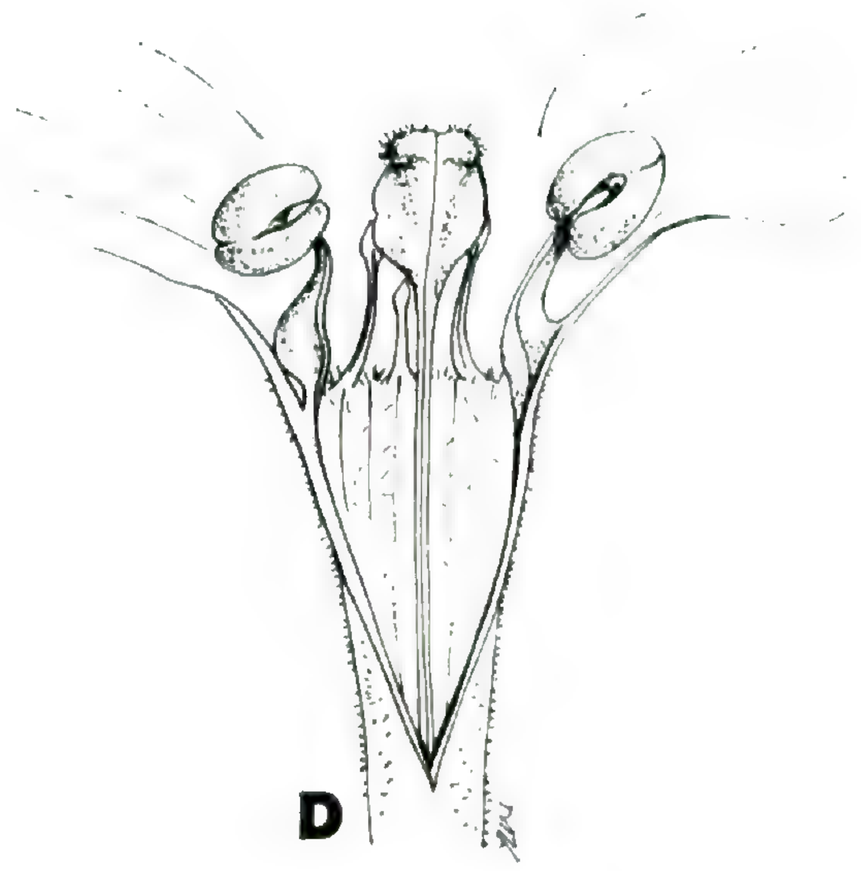
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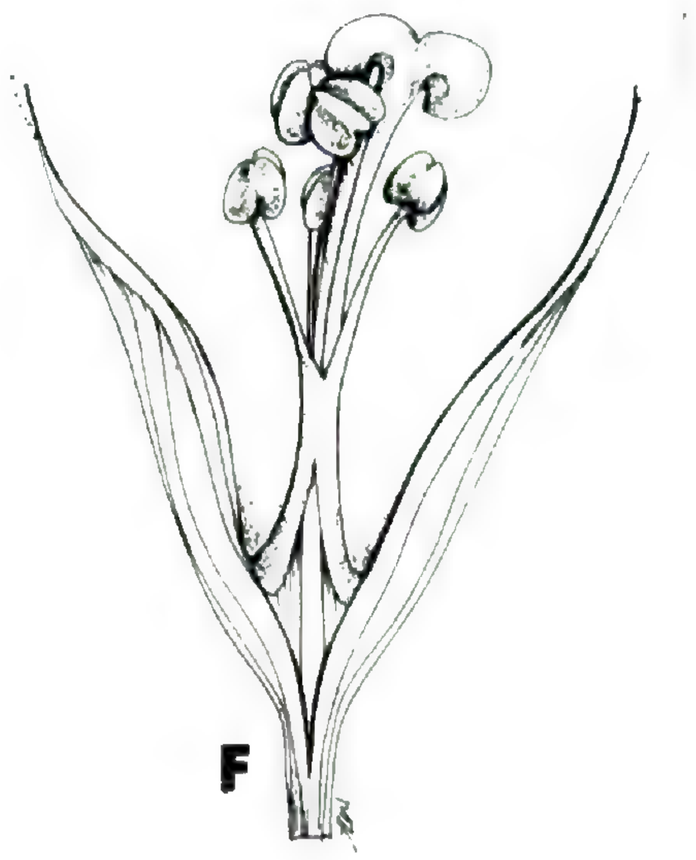
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TABLE 1. Specialization in flowers in the Cestreae.

Stage	General	Floral characters
I	*Cestrum* (sect. *Habrothanmus*) *Nicotiana* (subgen. *Rustica*) *Petunia*	Corolla regular. Corolla mouth open, anthers and stigma clustered loosely. Stamens 5, alike, inserted low in the tube. Stigma small, capitate or 2-lobed.
II	*Browallia* *Cestrum*[a] (sect. *Cestrum*) *Hunzikeria* *Leptoglossis* *Nicotiana* (subgen. *Petunioides*)[a] *Reyesia*	Corolla zygomorphic. Corolla mouth narrow, anthers and stigma tightly packed. Stamens 4(5), didynamous, inserted high in the tube, some anthers reduced. Stigma elaborated, sometimes 2-armed.
III	*Nicotiana* (subgen. *Nicotiana*)[a] *Nierembergia* *Salpiglossis*	Corolla slightly zygomorphic. Corolla mouth open, anthers and stigma clustered loosely or exserted. Stamens 4(5), inserted low in the tube, some anthers reduced. Stigma elaborated.

[a] Group does not have all characters of this stage.

had flowers somewhat like those of Stage I. Whether the genera with Stage II or Stage III were all derived directly from Stage I or pre-Stage I ancestors or whether they arose sequentially is not clear. But it is quite artificial to associate genera in the tribe which have undergone stamen reduction, as such genera now represent endpoints in discrete lines of evolution, some of them perhaps of considerable antiquity and stemming directly from primitive stocks.

DISTRIBUTION AND DISJUNCTION

Tribe Cestreae includes about 500 species in 15 genera occurring in North and South America, Australia, and Africa (Table 2). The greatest proportion of

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FIGURE 1. Floral evolution in the Cestreae, all views slightly exploded.—A–D. Stage II, the anthers and stigma fitting tightly to close the constricted corolla mouth.—A. *Browallia americana* L. Only the pubescent filament apices are visible from the outside (×5). [After *Gentry 4459* (OKLA).]—B. *Hunzikeria texana* (Torr.) D'Arcy. Only the apical rim of the stigma is visible from the outside. The basal portion of the stigma has been referred to as wings (×10). [After *Wynd & Mueller 140* (MO).]—C. *Leptoglossis linifolia* (Miers) Griseb. Only the apex of the stigma is visible from the outside. A staminode is present. The basal portion of the stigma has been referred to as wings (×8). [After *O. Kuntze* 16 Jan. 1892 (NY).]—D. *Reyesia chilensis* Clos. Because the flower is so small, the anthers and stigma are tightly appressed, although there is no constriction of the corolla tube. The stamens are clearly didynamous. [After *Werdermann 156* (MO).]—E–F. Stage III, evolution beyond the levels of the other genera.—F. *Nierembergia angustifolia* H.B.K. The filaments are partly fused and both stigma and anthers are exserted. All anthers are alike but differ in size, and the style is conspicuously 2-armed. (×10). [After *Rzedowski 22072* (TEX).]—E. *Salpiglossis erecta* (Dun.) D'Arcy. The stamens are only 4 and the anthers are somewhat unequal in size. The style has definite arms. (×6). [After *Lindheimer 471* (MO).]

TABLE 2. Distribution of the Cestreae.

Genera	N. America Mainly temperate	S. America Mainly temperate	American Mainly tropical[a]	Other (Australia, Africa)
Benthamiella	—	10	—	—
Browallia	—	—	2	—
Brunfelsia	—	—	25	—
Cestrum	few	few	175	?
Combera	—	2	—	—
Fabiana	—	25	—	—
Hunzikeria	2	—	1	—
Leptoglossis	—	3	—	—
Nicotiana	9	30	—	21
Nierembergia	1	35	—	—
Petunia	1	40	2	—
Reyesia	—	5	—	—
Salpiglossis	2	3	—	—
Sessea	—	—	5	—
Streptosolen	—	—	1	—
Total	ca. 18	ca. 155	211	21

[a] Does not include upland Peru, Ecuador, Mexico, Guatemala.

species is of the New World, only about 21 species of *Nicotiana* occur in Australia and 1 species in South West Africa. The greatest diversity is in South America where 14 genera occur, 5 of them endemic. Eight genera occur in North America, none of them endemic. In total species the tribe is about equally tropical and temperate, but in genera the tropics are poorly endowed, only 6 genera occurring there and only 4 of these endemic. The majority of tropical species are in the widespread genus *Cestrum*, which has a few species ranging into the temperate zones. D'Arcy (1973, 1975) noted that the most primitive members of *Cestrum* sect. *Habrothamnus* occur in Mexico.

Four genera are disjunct between North and South America with no species native in the intervening tropical regions of Central America, Colombia, or lowland Peru and Ecuador. *Nicotiana*, *Nierembergia*, *Petunia*, and *Salpiglossis* have the majority of their species in South America with a minority of species disjunct northward. The several workers, e.g., Raven (1962, 1963) and Solbrig (1972) who have written about North-South American disjunctions have not noted the disjunction in this group. None of these plants has fruits adapted for ingestion by birds; they all have minute seeds in dry capsules. Such seeds might be transported on the feet of birds. In some cases the species are little different from their disjunct counterparts, but in other cases there has been substantial divergence. For example, in *Nicotiana*, sects. *Bigelovianae*, *Nudicaulis* and *Trigonophyllae* of subgenus *Petunioides* are endemic in North America. The most primitive subgenus, *Rustica*, is endemic to South America. Because there is endemism at several levels on both continents, it is likely that stocks have moved at different times over long periods of time. South America would appear to be the ancestral region for the Cestreae, as here is where the greatest generic diversity occurs, and in South America there is also diversity in other subfamilies in the Solanaceae.

Review of Genera

The following review discusses genera in the order of floral specialization suggested in Table 1. North American groups are more fully treated than those of South America, and for some of the large genera, only the species of North America are noted in detail. Besides the genera noted here, the Cestreae embraces *Brunfelsia* of lowland tropical America and six other genera endemic to South America: *Benthamiella*, *Combera*, *Fabiana*, *Phrodus*, *Sessea*, and *Streptosolen* (see Table 2). Keys separating most of the genera were presented by Wettstein (1895), Bentham & Hooker (1876), and Millán (1931). The following key notes differences believed to be diagnostic.

a. Corolla mouth open, the anthers and stigma clustered loosely at the mouth; stamens inserted low in the tube.
  b. Stamens 5, all thecae alike; stigma minute, obscurely 2-lobed.
    c. Fruit a berry; plants mostly woody ..... 1. *Cestrum*
    cc. Fruit a dry capsule; plants mostly herbaceous.
      d. Flowers solitary; upper leaves appearing opposite ..... 3. *Petunia*
      dd. Flowers in inflorescences; all leaves alternate ..... 2. *Nicotiana*
  bb. Stamens 4(5), usually some thecae reduced; stigma elaborated, 2-armed or lamellar.
    e. Stamens often unequal but not in pairs ..... 9. *Salpiglossis*
    ee. Stamens clearly didynamous ..... 7. *Reyesia*
aa. Corolla mouth narrow, mostly plugged by the anthers and style; stamens inserted high in the tube.
  f. Stamens and style exserted; filaments partly connate ..... 8. *Nierembergia*
  ff. Stamens and style included or only minutely exserted; filaments free.
    g. Stamens 4, didynamous; fruit a capsule.
      h. Corolla cylindrical with a small limb; calyx narrow ..... 6. *Leptoglossis*
      hh. Corolla salverform with a large limb; calyx mostly broad.
        i. Corolla mouth closed by expanded filament apices; seeds numerous, less than 1 mm across, prismatic and evenly pitted ..... 4. *Browallia*
        ii. Corolla mouth closed by stigma; seeds few, more than 1 mm across, rounded and coarsely sulcate ..... 5. *Hunzikeria*
    gg. Stamens 5, often unequal but not in pairs; fruit a berry ..... 1. *Cestrum*

1. **Cestrum** L., Sp. Pl. 191. 1753; Gen. Pl., ed. 5. 88. 1754. TYPE: *C. nocturnum* L.

Cestrum, the largest genus in the tribe, is predominately tropical in distribution but several species range south as far as Chile and Uruguay and several range north as far as the southern United States and the Bahamas. Two sections are recognized, sect. *Habrothamnus* with about 30 species in eastern Mexico and ranging into Central America, and sect. *Cestrum* comprising the rest of the species. D'Arcy (1973, 1975) has postulated that sect. *Habrothamnus* is primitive. In this section, species have the most varied floral morphology, the calyx is larger, the corollas are larger and inflated, the anthers are longer, the stamens are inserted lower in the tube, the ovules are numerous, and the endosperm is distinctively colored (Francey, 1935). *Cestrum* is seemingly primitive in the tribe, and its immediate precursors may have been ancestral to some other genera in the tribe.

2. **Nicotiana** L., Sp. Pl. 180–1. 1753; Gen. Pl., ed. 5. 84. 1754. TYPE: *N. tabacum* L.

Nicotiana is a large genus with centers in Andean South America, Mexico, and Australia. The genus was monographed by Goodspeed (1954) and the Australian species were revised by Burbidge (1960). Goodspeed recognized three subgenera, the two most primitive, *Rustica* and *Nicotiana* being confined to western South America, and the most advanced, *Petunioides*, with representatives in North and South America and in Australia. Flowers of subgenus *Nicotiana* do not seem to have followed the pathway in floral evolution postulated for other genera discussed here. Some members of subgenus *Petunioides* of South America somewhat resemble *Leptoglossis*, especially in corolla shape, but the anthers are all alike, and while the filaments are sometimes unequal, they are not didynamous. Species of *Nicotiana* usually have a distinct throat between the tube and the limb, and this is not developed in either *Salpiglossis* or *Reyesia*. It is present in *Hunzikeria* and in *Leptoglossis*.

3. **Petunia** Juss., Ann. Mus. Natl. Hist. Nat. 2: 215, *tab. 47*. 1803. TYPE: *P. parviflora* Juss.

Petunia was revised by Fries (1911), who showed that it embraces about 40 species mainly of southeast Brasil with 1 species disjunct in North America. This disjunct species, *P. parviflora* Juss. also occurs in South America. It is the only species commented upon here.

In his monograph of *Nicotiana*, Goodspeed (1954) noted probable origins of *Petunia*, *Cestrum* and *Nicotiana*, suggesting that *Petunia* evolved from the most advanced ancestor of the group. Flowers of the widely cultivated *P. violacea* Lindl. resemble *Salpiglossis sinuata* Ruiz & Pavón discussed below but differ in having 5 perfect stamens and a small, unelaborated stigma.

3a. **Petunia parviflora** Juss., Ann. Mus. Natl. Hist. Nat. 2: 215, *tab. 47*. 1803. TYPE: Brasil, *Commerson* (P, not seen).

This species is unlikely to be confused with any others discussed here, for it has very leafy diffuse branches with the short, narrow leaves appearing to arise in fascicles. The tiny corollas are often concealed in the foliage and calyces. The stamens are alike although 2 anthers may be larger than the other 3. The stigma is 2-cleft as in other species of the genus, but it also tends to be radially broadened displaying a somewhat 2-armed appearance.

Petunia parviflora has a very wide, disjunct range, occurring in eastern warm temperate South America and in Mexico and the southern United States. A paludal weed, the seeds may be dispersed by mud on the feet of birds.

Because this species is well represented in many herbaria, usually correctly identified, no specimens are cited here.

4. **Browallia** L., Sp. Pl. 631. 1753; Gen. Pl., ed. 5. 278. 1754. TYPE: *B. americana* L.

Browallia is one of the few zygomorphic members of the Cestreae which is tropical in distribution. Nomenclature and other features of the genus were surveyed by D'Arcy (1973). In *Browallia*, the stamens are didynamous, the upper

pair much larger, and the corolla mouth is closed by broadly expanded, ciliate filament apices.

There are two species:

4a. **Browallia americana** L., Sp. Pl. 631. 1753. TYPE: Hort. Cliff. (BM, not seen, the original seed source was Panama [Miller, 1768, '*Browallia*']).—FIG. 1A.

4b. **Browallia speciosa** Hook., Bot. Mag. *tab. 4339*. 1947. TYPE: not seen.

5. **Hunzikeria** D'Arcy, Phytologia 24: 283. 1977. TYPE: *H. texana* (Torr.) D'Arcy.

This genus embraces plants of Texas and Mexico which have been known as *Leptoglossis*. A most unusual feature of *Hunzikeria* is the seed (Fig. 2B). Only about 5 seeds are present per capsule and they are 1.5 mm long, much larger than in most other zygomorphic Cestreae. They are ellipsoidal or subreniform, cuneiform along one side and with about 8 transverse sulci and rounded ridges. The corolla is much like that of a *Nierembergia* with which plants have been confused in the past. The calyx, androecium, and seed are quite distinct from *Nierembergia*. Impressed by details of the androecia, Gray (1877) allied these plants with *Leptoglossis schwenkioides* of Peru (see below), but *Hunzikeria* differs from *Leptoglossis* in many features. Notable are the pedicels which are subtended by normal leaves or lack bracts altogether, the 5 short, deltoid calyx lobes, the obconical calyx tube, the filiform, long-exserted corolla tube, the broad rotate limb, and the capsule included in the calyx tube. The seeds plus the salverform corolla and obconical calyx distinguish *Hunzikeria* from other genera of Solanaceae. It is interesting that somewhat similar, radially sulcate seeds are found in *Solanum lumholtziana* Bartlett, a species of northwestern Mexico (Whalen, 1977). This is a striking convergence of seed morphology in plants from different subfamilies.

5a. **Hunzikeria coulteri** (A. Gray) D'Arcy, comb. nov.—FIG. 2C.

Leptoglossis coulteri A. Gray, Proc. Amer. Acad. Arts 12: 165. 1877. TYPE: Mexico, Hidalgo, Zimapán, *Coulter 1346* (GH, not seen; K, duplicate).
Nierembergia coulteri (A. Gray) Hemsley, Biol. Cent.-Amer. 2: 437. 1882.

Whether *Hunzikeria coulteri* is taxonomically distinct from *H. texana* is uncertain. It is known to me only by the type; all other material I have seen with this determination has turned out to be *Salpiglossis*. The type collection was taken somewhat south of the apparent limits of *H. texana*. It is a more open, weaker plant with longer corolla tubes and perhaps slightly larger limb. The flowers may have been white. The calyces differ in that the intermediate vein to the sinuses divides below the middle and becomes 2 distinct veins distally. In all material seen of *H. texana*, this intermediate vein remains unified, at least until the upper ¾ of the calyx tube. The calyx lobes of *H. texana* appear to be relatively shorter.

MEXICO. Hidalgo: Zimapán, *Coulter 1346* (K).

5b. **Hunzikeria steyermarkiana** D'Arcy,[4] sp. nov. TYPE: Venezuela, *Pittier 6419* (NY, holotype).

Herb to ca. 20 cm tall; roots short; stems terete, slender, puberulent with short, weak, curved hairs, perhaps glandular. *Leaves* obovate, to 4 cm long, 13 mm wide, apically obtuse, basally narrowed into an elongate, narrowly winged petiole, the midvein evident with ca. 3 nerves on each side, above sparingly short-glandular pubescent, glabrate beneath, manifestly ciliate; petiole 5–15 mm long, winged upwards, keeled at the base. *Inflorescences* solitary flowers at the tips of branches; pedicels glandular tomentose, slightly angled, ca. 3 mm long, becoming 5–7 mm long in fruit; bracts wanting. *Flowers* apparently held erect; calyx campanulate to obconical, 5-lobed, ca. 4 mm across, 5 mm long, slightly longer in fruit, glandular pilose outside, the tube 10-nerved, the lobes obtuse or deltoid, glabrate within; corolla salverform, drying mauve, the tube slender, to 10 mm long, exserted from the calyx, puberulent outside, longitudinally nerved, the limb rotate, to 15 mm across; stamens 4, didynamous, the anthers all alike, fertile; style apically winged, the stigma flat, cordate or rectangular, with 4 shallow grooves to accommodate the upper and lower anthers. *Capsule* included in the calyx.

This species differs from *H. texana* in its smaller corollas with shorter, relatively broader tubes, and in having all anthers alike, not reduced. The foliage is glabrate except on the margins, whereas in *H. texana* leaves are pubescent all over.

Hunzikeria steyermarkiana is known only from the subdesert area of Venezuela near the Caribbean coast just west of Caracas. It is named in honor of Julian Alfred Steyermark, an outstanding student of the Venezuelan flora.

VENEZUELA. CARABOBO: El Palito near Puerto Cabello in the cactus formation, 0–30 m, *Pittier 6419* (NY). Guaremales, road from Puerto Cabello to San Felipe in forest, 0–100 m, *Pittier 8882* (GH, NY).

5c. **Hunzikeria texana** (Torr.) D'Arcy, Phytologia 34: 283. 1977.—FIGS. 1B, 2A, 2B.

Browallia (*Leptoglossis*) *texana* Torr., U.S. & Mexican Boundary 2(1): 156. 1859. LECTOTYPE: Texas, *Wright 535* (NY; BM, F, G, MO, NY, P, TEX, isolectotypes).
Nierembergia (*Leptoglossis*) *viscosa* Torr., U.S. & Mexican Boundary 2(1): 155. 1859. LECTOTYPE: Texas, *Wright 535* (NY; BM, F, G, MO, NY, P, TEX, isolectotypes).
Leptoglossis viscosa (Torr.) Millán, Darwiniana 5: 489. 1941.

Diminutive woody *perennials* to 20 cm tall, branching from a woody base; stems slender but soon woody, viscid pilose with dense short hairs. *Leaves* entire, obovate to oblanceolate, occasionally cuneate, mostly 10–20 mm long, 5–8 mm wide, apically obtuse or sometimes acute, basally acute or acuminate, the venation obscure, viscid pilose, slightly more so beneath, the margins and costas ciliolate; petiole mostly 2–5 mm long. *Inflorescences* solitary or paired terminal or sub-

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[4] *Hunzikeria steyermarkiana* D'Arcy, sp. nov. *Herba* parva, pubescens, glandulosa. *Folia* petiolata, ciliata, laminis glabris. *Flos* salverformis, staminibus quattuor, didynamis, antheris aequalibus, fertilis.

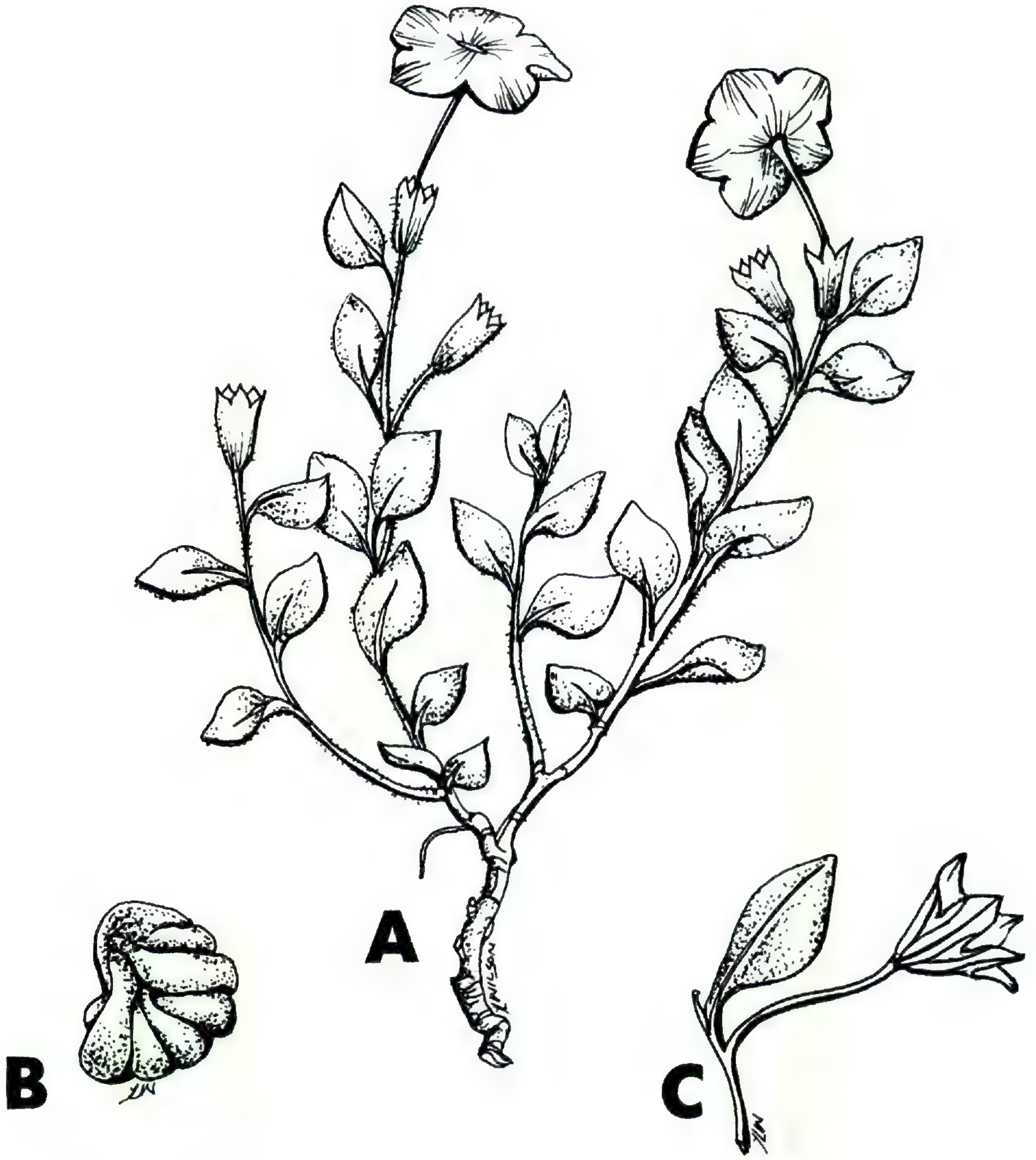

FIGURE 2. *Hunzikeria*.—A–B. *H. texana* (Torr.) D'Arcy.—A. Habit (×1). [After *Purpus 1911* (MO).]—B. Seed (×20). [After *Ripley & Barnaby 4183* (NY).]—C. *H. coulteri* (A. Gray) D'Arcy. Fruiting calyx (×1½). [After *Coulter 1340* (K).]

terminal flowers; pedicels terete, ca. 7 mm long, pilose, not accrescent, subtended by normal size leaves. *Flowers* with the calyx obconical, ca. 10 mm long, 10-nerved, pilose overall, scarcely accrescent, 5-lobed, the lobes deltoid, ca. 3 mm long; corolla "light-purple or purple-pink," salverform, pubescent outside with reduced hairs, the tube slender, 15–25 mm long, ca. 0.5 mm wide, scarcely expanded upwards, longitudinally nervate, the throat expanded around the anthers, ca. 2 mm long, the limb rotate, 20–23 mm across, slightly oblique on the tube, 5-lobed ca. halfway down, the lobes nearly regular, rounded-obtuse, the mouth tightly constricted around the stamens; stamens 4, the filaments inserted low in

the tube, the upper (ventral) pair of anthers much reduced, situated slightly above the lower pair, a filiform staminode sometimes present; style 2-winged just below the stigma, the stigma crescentic-2-armed, included and compressed by the anthers. *Capsule* included in the calyx tube, "2-valved," ca. 5 seeded, the seeds large, ca. 1.5 mm long, oblong, with ca. 8 coarse, transverse furrows, reddish, the furrows darker than the ridges.

The pubescence of this species consists of short, slender, uniseriate hairs 2–3 cells long. The basal cell is much broader than those above, and the apical cell usually oozes a small drop of sticky fluid. Some details of the above description were taken from Correll (1970).

Correll and various collectors' notes indicate that this species grows mainly on rocky, limestone slopes and ranges along the eastern side of the Edwards Plateau and the Sierra Madre Oriental. The Schott collection from Chihuahua is well to the west of this upland, and the type collection of *H. coulteri* (see above) is both south and west of it. Correll indicated that the species flowers from May to June in Texas; in Mexico, flowering collections have been taken in nearly every month of the year.

UNITED STATES. TEXAS: Devil's River, *Bigelow* (NY). Kinney Co., Anacacho Ranch, Anacacho Mountains, *Correll & Rollins 32549* (TEX). 30 airline mi N of Del Rio, *Cory 41529* (TEX). Valverde Co., Pecos River below bridge on Highway 90, 1200 ft, *Hinckley & Hinckley 413* (TEX, US). Valverde Co., Devil's Lake, ca. 20 mi NNW of Del Rio, *McVaugh 7733* (F, TEX). West Texas, *Neally* 1890 (F). Valverde Co., Devil's River, *Orcutt 6036* (MO). Valley of Rio Grande near Donana, *Parry et al. 630* (NY). Valverde Co., 3 mi E of mouth of Pecos River, *Ripley & Barnaby 4183* (NY). On Bravo del Norte, *Schott* 1852 (F). Without locality, *Thurber* 1850–52 (F). Del Rio, *Whitehouse* 4/1/33 (TEX). Expedition from western Texas to El Paso, New Mexico, *Wright 535* (BM, F, G, MO, NY, P, TEX).

MEXICO. CHIHUAHUA: *Schott* (F). COAHUILA: 2 km SW of Rancho San Miguel WSW of Cuidad Acuna, *Chiang et al. 7502* (TEX). Saltillo-Piedras Negras road, *Crockett 8125, 8129* (both TEX). Sierra de la Rata, 550–1700 m, *Johnston et al. 10160F* (TEX). 1 km N of Rancho de la Gavia on N side of Sierra de la Gavia, 1200 m, *Johnston et al. 10276A, 10277* (both TEX). Cañon Bonanza, SE end of Sierra de la Purisima, 1300–1650 m, *Johnston et al. 10296A* (TEX). Muzquiz, *Marsh 133* (TEX), *1046, 2110* (both F, TEX). Sierra de Gloria near Monclova, *Ripley & Barnaby 14215* (NY). NUEVO LEÓN: 5 mi S of Monterrey, *Barkley et al. 16M367* (TEX). Chipinque, *Barkley et al. 7153* (TEX). Monterrey, *Edwards & Eaton 1846* (NY). Punta de la Loma, 1700 m, *Etchison 19* (TEX). Monterrey, 1800 ft, *Fischer* 26 July 1926 (TEX). Near Monterrey, *Johnston & Barkley 16057M* (F, MO, TEX). Road to Chipinque Mesa S of Monterrey, 2000 ft, *Johnston & Crutchfield 5298* (TEX). Monterrey river valley, *Kenoyer* 18 Sept. 1937 (MO). Monterrey, *Kenoyer 1142* (F, MO); *Lacas 41* (F). Diente Canyon, near Monterrey, *Mueller & Mueller 176* (F). Opposite mouth of Diente Canyon, *Muller 2695* (TEX). Near Monterrey, *Pringle 1924* (BM, F, MO, MPU, NY, P), *2687* (F). 3 mi W of Monterrey, *Rollins & Tryon 5881* (TEX). Monterrey, *Smith M134, M202* (both TEX); *Webster & Aguirre 2955* (TEX). SAN LUIS POTOSÍ: N of Minas de San Rafael, *Chiang et al. 8172* (TEX). Minas de San Rafael, *Purpus 5012* (BM, F, MO, NY). TAMAULIPAS: Cañon de la Tamaulipeca, San Miguel, *Bartlett 10650* (TEX). 6 mi N of Santander Jiménez, 800 ft, *Johnston 4897* (TEX). 4 mi S of San Carlos on road to Padilla, *Johnston & Crutchfield 4998B* (TEX). Los Coyotes, *LeSueur 628* (F, TEX). Matamoros-Victoria Highway, *Richardson 1417* (TEX). Sierra between Jaumave and Victoria, *Rozynski 157, 477* (both F).

6. **Leptoglossis** Benth., Bot. Voy. Sulphur 143. 1844. TYPE: *L. schwenckioides* Benth., non *Leptoglossum* Karsten (1879, fungi).

Cyclostigma Phil., Sert. Mendoc. Alt. 39. 1871. TYPE: *C. tenue* Phil., non *Cyclostigma* Hochst. ex Endl. 1842 (Apocynaceae), nec Klotsch in Seem., 1853 (Euphorbiaceae).

Leptofeddea Diels, Repert. Spec. Nov. Regni Veg. 16: 193. 1919. TYPE: *L. lomana* Diels.

The name *Leptoglossis* should apply only to three (perhaps more) species of western South America. Plants of North America formerly known as *Leptoglossis* are referred to *Hunzikeria*. In *Leptoglossis* the stamens are didynamous, much as in *Browallia* and *Hunzikeria*, but the corolla tube is usually broadly cylindrical with a small limb, and the calyx is narrow with conspicuously differentiated ribs. The stigma is elaborated and compressed, much as in the related genus *Brunfelsia*. The seeds are numerous, prismatic and finely tuberculate. The glandular-pubescent plants range from diminutive ephemerals to shrubs attaining a meter in height. The flowers are solitary or aggregated into ill-defined racemes or panicles, each flower subtended by a bract. *Leptoglossis* appears to be closely related to *Reyesia*, particularly to *R. cactorum* which occurs in the same part of South America. *Leptoglossis* was placed in synonymy under *Salpiglossis* by Wettstein (1895) but this is unjustified, as is placement of one species in *Schwenckia* by Grisebach. Alignment of *L. schwenkioides* with the two species below is provisional: they may be generically distinct.

6a. **Leptoglossis linifolia** (Miers) Griseb., Symb. fl. Argent. 241. 1879. (Transfer incorrectly attributed to Bentham & Hooker by Jackson, Index Kewensis 2: 63. 1894 [1895.]).—FIG. 1C.

Nierembergia linifolia Miers, London J. Bot. 5: 174. 1846; Ill. S. Amer. Pl. 1: 98, *tab. 20, fig. 1.* 1850. LECTOTYPE: Argentina, *Gillies* 835 (K).

N. linifolia var. *macrophylla* Dun. in DC., Prodr. 13(1): 587. 1852. TYPE: Mendosa, Argentina, *Gillies* (?K, not seen).

N. linifolia var. *parviflora* Dun. in DC., Prodr. 13(1): 587. 1852. TYPE: Cordova, Argentina, *Gillies* (?K, not seen).

Cyclostigma tenue Phil., Sert. Mendoc. Alt. 39. 1871. TYPE: Mendoza, Chile (Argentina), *Phillipi* (G, W, neither seen; photos MO).

Schwenkia tenuis (Phil.) Griseb., Pl. Lorentz. 166. 1874.

Salpiglossis linifolia (Miers) Wettst. in Engl. & Prantl, Nat. Pflanzenfam. 4(3b): 36. 1891.

Leptoglossis tenuis (Phil.) Jackson, Ind. Kew. 2: 63. 1894 (1895), transfer incorrectly attributed to Bentham & Hooker.

L. schwenkioides var. *linifolia* (Miers) Monachino in Moldenke, Lilloa 5: 435. 1940.

L. schwenkioides var. *tenuis* (Phil.) Monachino in Moldenke, Lilloa 5: 435. 1940.

Leptoglossis linifolia is a small perennial reaching 12 cm tall. The leaves are smaller than in *L. schwenkioides*, although the pubescence is similar. The flowers are terminal, not forming differentiated panicles or racemes.

This species occurs in northwest Argentina.

The collection by Bruch-Carette cited below is a wiry plant of much sturdier construction than others; it may be taxonomically distinct.

ARGENTINA. Pampas Reise, *Kuntze* 16 Jan. 1892 (MO, NY). Pampas, W 34°, *Kuntze* 16 Jan. 1892 (NY). Banda oriental, *Tweedie 1837* (K). BUENOS AIRES: Cañada de Lucas, Pampas B. Ayres, *Gillies* 835 (K). CÓRDOBA: Córdoba, *Grisebach comm.* 1878 (K). SAN JUAN: Río San Juan, *Cuezzo 1284* (TEX). SAN LUIS: Alto Pencoso, *Bruch-Carette* Feb. 1914 (NY). San Luis, *Lorentz & Hieronymus* 1873 (NY). Santa Rosa, 650 m, *Varela 472* (NY). SANTIAGO DEL ESTERO: Loreto, *Cuezzo 2341* (TEX). Pinso, *Kuntze* Oct. 1892 (NY). Turena, Robles, *Maldonado 254* (NY). Dept. La Banda, Dique Lod. Quirogas, *Meyer 12804* (MO). TUCUMÁN: 5 km N de Tapia, *Krapovikas et al. 27877* (MO). Chañar Pozo, 300 m, *Venturi 5439* (A).

6b. **Leptoglossis lomana** (Diels) Hunziker, Kurtziana 10: 46. 1977.—FIG. 3B.

Leptofeddea lomana Diels, Repert. Spec. Nov. Regni Veg. 16: 193. 1919. TYPE: Peru, *Weberbauer 1486* (B, if extant, not seen; photo MO).

Salpiglossis linearis Johnston, Contr. Gray Herb. 81: 96. 1928, non *S. linearis* Hook. 1831. TYPE: Peru, *Pennell 13063* (GH, not seen; US, isotype).
S. albiflora Johnston, Contr. Gray Herb. 85: 178. 1929. TYPE: Peru, *Weberbauer 7424a* (GH, MO, NY, US).
S. acutiloba Johnston, Contr. Gray Herb. 85: 179. 1929, based on *Salpiglossis linearis* Johnston.
S. lomana (Diels) Macbride, Field Mus. Nat. Hist., Bot. Ser. 13(5b)(1): 143. 1962.

This species is an ephemeral herb attaining only ca. 15 cm. The leaves are oblanceolate, to 2 cm long, and on herbarium specimens, the rotund cotyledons are often persistent. The indumentum is of fine white hairs giving a greyish appearance. Flowers sometimes dry with a purplish or indigo cast.

Leptoglossis lomana occurs in sandy lomas and it ranges along most of the Peruvian coastal extent. There may be 2 species among the collections cited below which range from seaside to 2,600 m or higher.

PERU. AREQUIPA: 2 km S of Chala, 200 m, *Hutchison 1298* (F, NY). S of Mollendo, 15 m, *Mexia 04176* (MO), *7776* (F). Tiabaya, 2100–2200 m, *Pennell 13036* (NY, US), *Pennell 13081* (GH). Tingo, *Pennell 13119* (GH, NY). Jura, 2600 m, *Vargas 7984* (MO). CAJAMARCA: Portachuelo, 850 m, *Sagástegui et al. 7528* (MO). LIMA: Ambar, 2010 m, *Stork 11438* (GH). San Bartolomé, Lima-Oroyo railroad, 1500–1600 m, *Weberbauer 5297* (GH). MOQUEGUA: Mt. Estiquina NW of Moquegua, *Weberbauer 7424a* (GH, MO, NY, US).

6c. **Leptoglossis schwenkioides** Benth., Bot. Voy. Sulphur 143. 1844. TYPE: Peru, Barclay (K).—FIG. 3A.

L. schwenkioides var. *typica* Monachino in Moldenke, Lilloa 5: 435. 1940.
Salpiglossis schwenkioides (Benth.) Wettst. in Engler & Prantl, Nat. Pflanzenfam. 4(3b): 36. 1895.

This species is a shrub with numerous, entire, small or even scalelike leaves, reduced upwards. The flowers are numerous in the upper branches, subtended by small bracts and aggregated into poorly defined racemes and panicles. The calyces are more or less campanulate with 5 narrow lobes and evident membranous sinus areas. The corollas are cylindrical, mostly 1.0–1.5 cm long, and the tube is 1.0–1.5 mm wide. The throat tightly envelops the stamens and the limb is small.

Leptoglossis schwenkioides occurs in canyons above Lima.

PERU. LIMA: Lima, *Cumming 1010* (K). Above Sta. Eulalia, 1200 m, *Goodspeed 33098* (GH, MO). Canta Valley NE of Trapiche, *Hutchison 1032* (F, MO, NY). AMBAR: *Stork 11455* (GH). San Bartolomé, *Weberbauer 5290* (F, GH).

7. **Reyesia** Clos in Gay, Fl. Chil. 4: 418, *tab.* 52. 1849. TYPE: *R. chilensis* Clos.

Pteroglossis Miers, Ann. Mag. Nat. Hist., ser. 2, 5: 32. 1850, non *Pteroglossa* Schlecht, 1920 (Orchidaceae). TYPE: *P. laxa* Miers = *Reyesia laxa* (Miers) D'Arcy.

Although *Reyesia* was recognized by Bentham & Hooker (1876), Wettstein's (1892, 1895) placing of this genus into *Salpiglossis* relegated it to obscurity until recently revived by Hunziker (1977). *Reyesia* is closely related to *Salpiglossis* as evidenced by its similar corolla shape and 2-armed stigma, but the didynamous stamens, sometimes pubescent filaments, and the persistent winged placenta in fruit are quite distinct. This winged placenta resembles that in *Lindernia*, Scrophulariaceae. An interesting feature is the pair of small wings on the style just below the stigma which is reported in *Reyesia chilensis* and in *Hunzikeria texana*. This is the lower half of a laminar style as is seen in *Leptoglossis* (Fig. 1C).

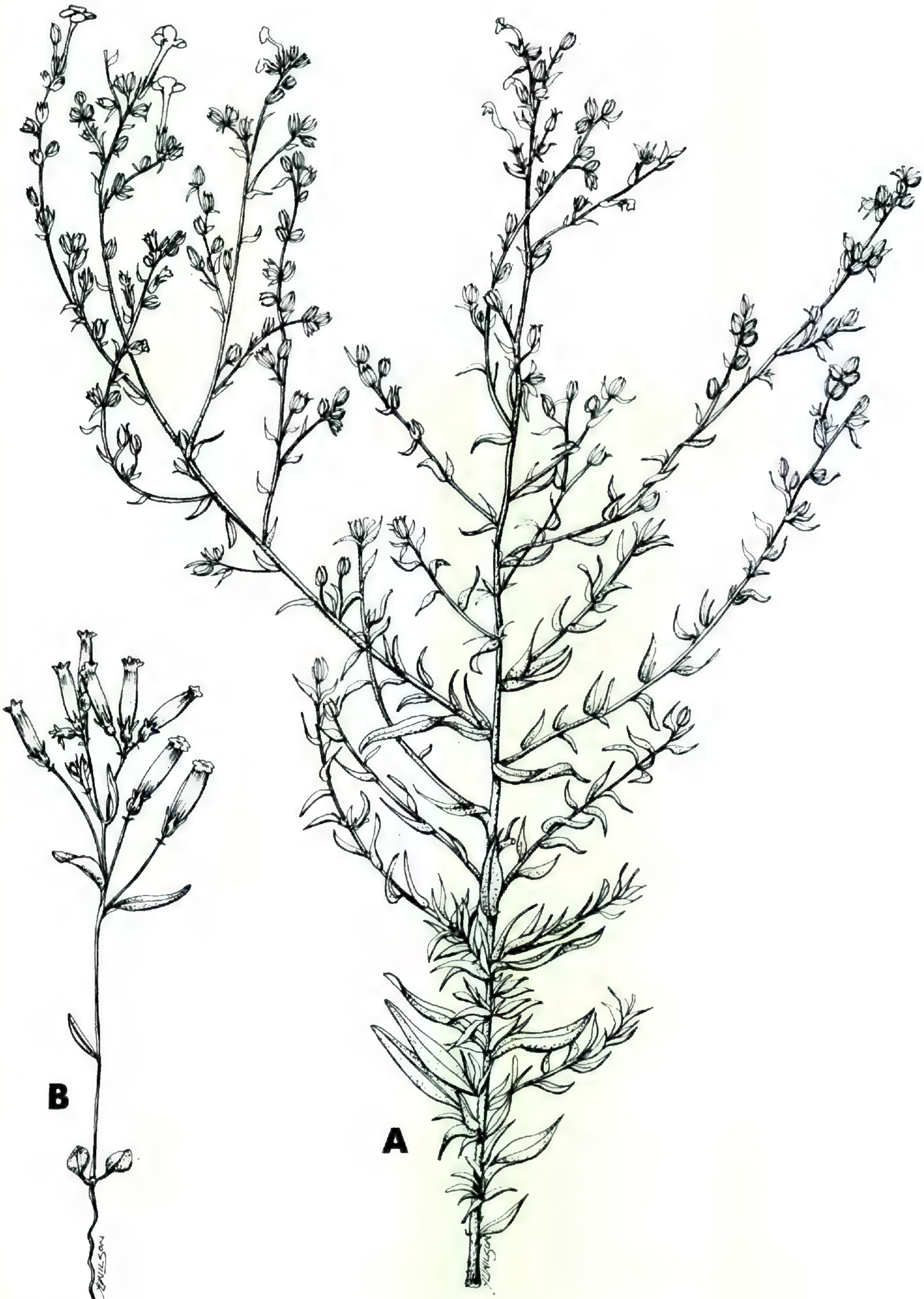

FIGURE 3. *Leptoglossis*.—A. *L. schwenckioides* Benth. Habit (×⅗). [After *Hutchison 1032* (MO).]—B. *L. lomana* (Diels) Hunziker. Habit (×1⅕). [After *Mexia 04176* (MO).]

In the four species of *Reyesia* known to me, the corolla is minute, the stems slender and nearly leafless, and the lower leaves are sometimes undulate or lobed as in species of *Salpiglossis*. All species are from northern or central Chile.

7a. **Reyesia cactorum** (Johnston) D'Arcy, comb. nov.

Salpiglossis cactorum Johnston, Contr. Gray Herb. 85: 114. 1929. TYPE: Chile, *Johnston* 5258 (US).

This species, which is from the same area as *Reyesia chilensis*, differs in having tomentulose stems, pilose petioles, bipinnatifid leaves and flowers to 15 mm long, twice as large as in *R. chilensis*. The corolla lobes appear to be rotate.

CHILE. Antofagasta, Dept. Taltal, near Aguada de Chardon, *Johnston* 5258 (US).

7b. **Reyesia chilensis** Clos in Gay, Fl. Chil. 4: 418, *tab.* 52. 1849. TYPE: Chile, *Gay* (K, P, not dissected).—FIG. 1D.

Salpiglossis chilensis (Clos) Wettst. in Engl. & Prantl, Nat. Pflanzenfam. 4(3b): 36. 1895.
S. brachysiphon Johnston, Contr. Gray Herb. 85: 161. 1929. TYPE: Chile, Antofagasta, hills near Tocopilla, *Johnston* 3625 (GH, not seen).

Much-branched *perennial* from a woody base; stems wiry, puberulent. *Basal leaves* oblanceolate, 4–5 cm long, 5 mm wide, shallowly lobed or entire, the costa prominent beneath, narrowed to an elongate petiole, glabrate; *cauline leaves* mostly reduced to linear scales. *Inflorescence* of scattered terminal or subterminal flowers; pedicels filiform, apically glandular, subtended by scalelike bracts. *Flowers* 6–7 mm long, narrow; calyx 5-lobed, 2 mm long, campanulate or slightly urceolate, the lobes acute, the costas continuous from the tube, contrasting with the sinus areas; corolla white, drying conspicuously bluish-nervate, the tube expanding gradually, the limb campanulate, short-lobed; stamens 4, didynamous, the filaments pubescent; style apically winged, the stigma 2-armed. *Capsule* 4-valved, the valves about equalling the calyx lobes; seeds minute.

In spite of the size and branching difference noted by Johnston, the type of *Salpiglossis brachysiphon* is well within the variation of other material seen of *Reyesia chilensis*.

This species is notable for its numerous, nearly leafless wiry stems and minute flowers. It occurs in central Chile.

CHILE. ANTOFAGASTA: Tocopilta, *Jaffuel 1003* (GH); *Johnston 3625* (GH). Hills SE of Taltal, *Johnston 5084* (GH). Taltal, *Johnston 5650* (GH). 5 km SE of Taltal, 200 m, *Morrison 17095* (MO). Taltal, 100 m, *Werdermann 821* (MO, NY). ATACAMÁ: Desert of Atacamá, *Geisse 170* (NY). Alto del Carmen, Vallenar, 800 m, *Werdermann 156* (GH, MO). 3 km SW of Huasco, *Worth & Morrison 16243* (GH). COQUIMBO: Tres Cruces, Serena, *Muñoz 325* (GH).

7c. **Reyesia juniperoides** (Werderm.) D'Arcy, comb. nov.

Salpiglossis (*Reyesia*) *juniperoides* Werderm., Notizbl. Bot. Gart. Berlin 10: 474. 1928. TYPE: Chile, *Werdermann 1054* (B, if extant, not seen; F, GH, MO, NY, US, isotypes).

Robust, profusely branched glabrate *shrub*; stems slender, rigidly woody, the internodes short, appearing leafless. *Cauline leaves* reduced to sublinear, cuculate scales to 1 mm long. *Flowers* solitary, scattered on the upper branches; calyx

narrow, 5-lobed about halfway down; corolla ca. 7 mm long, the tube narrowly ascending upwards, the throat small, differentiated, the limb ellipsoidal in bud; stamens 4, didynamous; stigma 2-armed. *Capsule* indurate, stramineous, 2- or 4-valved, the placenta peglike, winged by the broad dissepiment.

Reyesia juniperoides is superficially much like *R. chilensis*, but the branching is much sturdier, subspinose, and the corolla tube is relatively longer and narrower. It is known only from central Chile.

CHILE: Tarapaca, Cordillera Quebrada de Quipisca, Palca, 2500 m, *Werdermann 1054* (F, GH, MO, NY, US).

7d. **Reyesia laxa** (Miers) D'Arcy, comb. nov.

Pteroglossis laxa Miers, Ann. Mag. Nat. Hist., ser. 2, 5: 33. 1850; Ill. S. Amer. Pl. 2: 62, *tab.* 52. 1857. TYPE: Coquimbo, *Bridges 1839* (K, not seen).
Salpiglossis parviflora Phil., Viaj. Des. Atacamá 219. 1860. TYPE: Coquimbo, Chile, *Philippi* (SGO, not seen; photo (poor) GH; dupla B if extant, photo MO).
Reyesia parviflora (Phil.) Hunziker, Kurtziana 10: 46. 1977.

In this species the stems are less wiry and less intricately branched than in the preceding species. The basal leaves are obovate, crenately lobed, 3–5 cm long forming a rosette. The corolla, ca. 8 mm long, has a broader tube and the throat is less differentiated.

Reyesia laxa is known only from the hillsides of central Chile and adjacent Argentina (San Juan Province).

ARGENTINA. SAN JUAN: Near Baños San Crespin, 3300 m, *Johnston 6115* (GH). Río de la Tagua below junction with Río de la Sal, 2900 m, *Johnston 6146* (GH).

CHILE. Baños del Toro, 3500 m, *Werdermann 195* (GH, MO). ATACAMÁ: Molle, *Geisse* 1889–1890 (GH). Quebrada de Doña Ines, Chañaral, *Gigoux* 1886 (GH). Potrerillos, 2800 m, *Johnston 4743* (GH). COQUIMBO: Río Toro above Los Baños, 3300 m, *Morrison 17266* (GH, MO). Río Seco, 14 km E of Nueva Elqui, *Wagenknecht 18119* (MO). 98 km from Rivadavia to Laguna Dam, 2900 m, *Worth & Morrison 16399*.

8. **Nierembergia** Ruiz & Pavón, Fl. Peruv. Chil. Prodr. 23. 1794. TYPE: *N. repens* Ruiz & Pavón.

Nierembergia embraces about 35 species of Argentina and Chile with 1 species disjunct in Mexico. The genus was revised by Millán (1940, 1941). In *Nierembergia* the corolla is salverform as in *Hunzikeria*, but the androecium consists of 5 similar stamens with filaments inserted at various levels but united at least in part to form a tube surrounding the style. The stigma is generally enlarged into a 2-armed or crescent-shaped process between or surmounting the anthers. Di Fulvio (1975b) reported that the pollen of some species is in tetrads. Only the Mexican species, *N. angustifolia*, is discussed here.

8a. **Nierembergia angustifolia** H.B.K., Nov. Gen. Sp. Pl. 3: 9, *tab. 198*. 1818. TYPE: Mexico, Real del Monte (not seen).—FIGS. 1F, 4.

Bouchetia procumbens DC. ex Dun. in DC., Prodr. 13(1): 389. 1852, based on Moçino & Sessé *plate 920* (G).

This species differs from most other species discussed in this paper in being

almost completely glabrous. It is widespread in Mexico, but collections are few. The corolla appears on the herbarium sheet much like that of *Hunzikeria texana*, but the androecium and gyneocium are quite different. The filaments in this species are connate below and free above, the united portion forming a short tube which is open along one side. The anthers are alike but differ in size and are situated in two groups, one slightly above the other. In this species the style arms are less developed than in many South American species, but they are present, contrary to observations of Millán.

For a discussion of the typification of *Bouchetia procumbens* and further notes on the morphology of this plant, see under *Salpiglossis*, below.

MEXICO. DURANGO: Near Durango, *Palmer 121* (C, F, MO). MEXICO: Laguna de Atenco, 2250 m, *Rzedowski 22072* (MSC, TEX). MICHOACÁN: Near Morelia, *Pringle 4149* (F, KM, MSC, MO). PUEBLA: Laguna San Baltasar near Puebla, 2135 m, *Arsène 292* (MO). SAN LUIS POTOSÍ: Near San Luis Potosí, *Parry & Palmer 630* (BM, F, K, MO). WITHOUT LOCALITY: Ex herb. *Sessé & Moçino* (F).

9. **Salpiglossis** Ruiz & Pavón, Fl. Peruv. Chil. Prodr. 94, *tab. 19*. 1794. TYPE: *S. sinuata* Ruiz & Pavón.—FIG. 1E.

Bouchetia DC. ex Dunal in DC., Prodr. 13(1): 589. 1852. TYPE: *B. erecta* Dun. = *Salpiglossis erecta* (Dun.) D'Arcy.

Salpiglossis sinuata is a large-flowered species from central Chile which is frequently cultivated in temperate gardens for its showy flowers. This species grows to 1 m tall and may have flowers as large as 6 cm across. The upper leaves are entire but lower leaves may be sinuate. This species characterizes the genus *Salpiglossis* as having campanulate, often strongly nerved corollas, 4(5) similar stamens inserted low in the corolla tube and sometimes a staminode, and a somewhat expanded, 2-armed stigma grooved as if to accommodate the anthers at some earlier stage of growth or evolution. Sometimes one or more stamens is reduced but not in a definite pattern of didynamy as in some related genera. Traditionally *Salpiglossis* has included large-flowered horticultural plants and a heterogenous assembly of small-flowered plants, many of which belong to other genera. Wettstein (1895) placed elements of *Reyesia* and *Leptoglossis* in *Salpiglossis* and this has been followed by many workers, including Werdermann (1928) who treated the genus for Chile. I remove discordent elements from *Salpiglossis* and bring plants hitherto known as *Bouchetia* into *Salpiglossis*.

Typification of Bouchetia.—Bouchetia is here placed into synonymy under *Salpiglossis*, but because of its long use for plants in both North and South America, a discussion of its typification is in order. The name *Bouchetia* honors Dominique Bouchet-Doumeng, an amateur botanist of Montpellier, who was born near Avignon in 1770 and died at Montpellier in 1845. *Bouchetia* was first described in the Solanaceae in de Candolle's *Prodromus* (1852) with two species, *B. procumbens* and *B. erecta*. The Solanaceae treatment of the Prodromus was written by M. F. Dunal of Montpellier, one of de Candolle's students. Although the names are generally attributed to de Candolle, Stafleu & Cowan (1976: 290) and the *Index Nominum Genericorum* cite Dunal as the author. Dunal himself attributed the treatment of *Bouchetia* in the *Prodromus* to de Candolle "DC. mss."

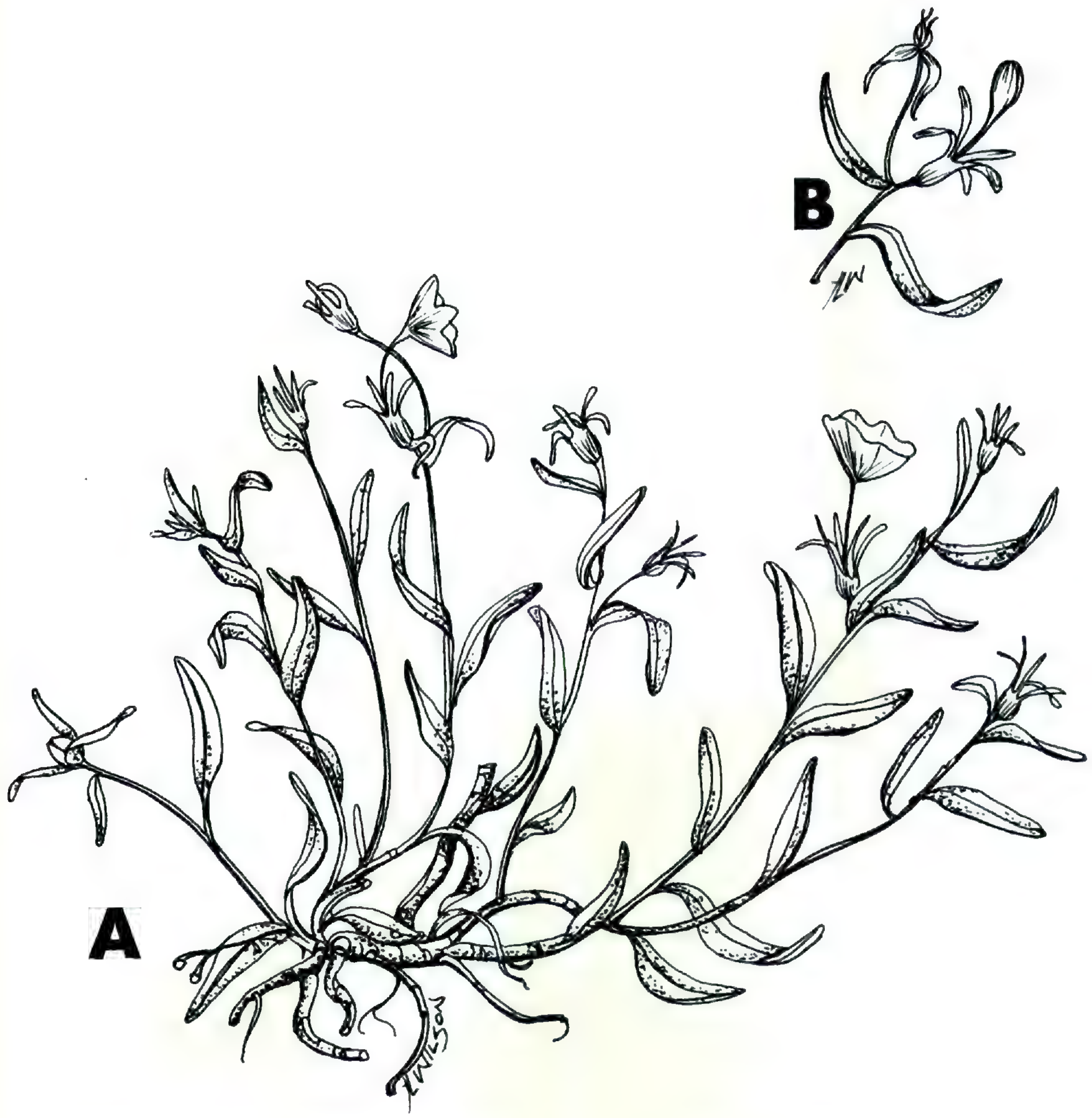

FIGURE 4. *Nierembergia angustifolia* H.B.K.——A. Habit (×2).—B. Flower bud (1½). [After *Palmer 121* (MO).]

Although a number of elements are cited under the original description of *Bouchetia* and its two species, only material available to August Pyramus de Candolle is directly relevant for typification. Under *B. procumbens*, only plate no. 920 of Moçino & Sessé is cited. Under *B. erecta*, plate no. 921 of Moçino & Sessé is cited as well as several other elements including some specimens. These plates are part of a series of colored illustrations of Mexican plants brought by José Mariano Moçino to Montpellier in 1815 when he fled Spain for political reasons. De Candolle and his student Dunal studied these plates and de Candolle was able to obtain part of the corresponding text which had been seized in Spain and stored in a cave in Paris (A. P. de Candolle, 1862). Some of the plates were copied in Montpellier by Node Véran, a noted artist of the time who also prepared the plates for Dunal's thesis on the Solanaceae. In 1816 de Candolle left Mont-

pellier for Geneva and at the urging of Moçino, who was in failing health, took the plates with him. Shortly after de Candolle's installation at Geneva, Moçino had a change of heart and demanded the plates back. De Candolle hurriedly assembled a group of townspeople to copy the remaining plates before the originals were returned. The product is of variable quality, some of the copies being fine, colored works and probably close renditions of the originals, while others are crude, and many are unfinished. The copies are now in Geneva, but the originals returned to Moçino have since disappeared. In 1874, Alphonse de Candolle, the son who was editor of the final volumes of the *Prodromus*, had tracings made of the Geneva copies and distributed them as the Calques des Dessins (A. L. P. P. de Candolle, 1874). This convoluted history of the Sessé-Moçino plates is significant to typification of *Bouchetia*.

The two Moçino & Sessé copies cited under *Bouchetia* agree well with the diagnoses, but the amplified description of *B. erecta* includes details which are not evident on the copies, e.g., caules puberuli, folia ciliata, pedunculus pubescenti-hirsutus. These details may have been present on the Moçino originals or gleaned from the corresponding text, or they may have been added by Dunal from the specimens he cited.

The first element cited under *Bouchetia erecta* is a specimen in the de Candolle herbarium collected in Texas by Wright. Charles Wright collected in Texas in 1849 and a set of duplicates was personally delivered by Asa Gray to Alphonse de Candolle on a visit of 1850 (McKelvey, 1955). This was much too late for study by Augustin de Candolle, who died in 1841, but was probably not too late for study by Dunal before completing the Solanaceae treatment for the *Prodromus*. The Wright collection in the de Candolle herbarium is a mixture, the left-hand specimen corresponding to the diagnoses of *Bouchetia* and the right-hand specimen being a plant of *Hunzikeria texana*. The mixing was probably of Gray's doing, for he generally ignored Wright's field numbers and assembled similar plants into sets for sale (McKelvey, 1955).

Also cited under *B. erecta* is a crude, highly stylized drawing of three erect, narrow-leaved stems with a thick root referred to as *Itzticapitli* in Francisco Hernandes' 1651 volume on Mexican medicinal plants. Although it bears little resemblance to the plants now identified with *Bouchetia*, this drawing is not unlike the Geneva copy of *Bouchetia erecta*, plate no. 921. In fact, the roots of the two plates are so much alike that I suspect that de Candolle's local artist looked to the Hernandes plate for assistance in copying the Moçino illustration.

Another specimen cited is a plant in the general herbarium at Geneva labeled *Maleolaria lanceolata* Pav., ex herb. Pav. This also corresponds to the *Bouchetia* diagnosis and appears to be the same species as the left-hand Wright collection. Finally, specimens cited as *Nierembergia* of the Wright herbarium have not been located.

The type of *Bouchetia erecta* is the Geneva copy of Moçino & Sessé plate no. 921 which represents a species of Solanaceae found in Mexico and Texas and perhaps in Argentina. Although I have seen no herbarium material with the large roots illustrated, they may well be present on entire plants. This species is here chosen as lectotype of the genus *Bouchetia*. Before submitting de Candolle's

first manuscript for inclusion in the *Prodromus*, Dunal was able to review actual specimens which helped confirm his acceptance of de Candolle's concept of *B. erecta*; no such review was possible for *B. procumbens*. This selection of lectotype maintains the concept of *Bouchetia* which subsequent authors have accepted. To choose *B. procumbens* as lectotype would break this tradition, as is outlined below.

Since the first description of *Bouchetia procumbens*, there have been discordant attempts to relate plate 920 to later collections. Bentham & Hooker (1876) identified the plate with two Mexican collections, *Galeotti 1476* and *Bourgeau 68* and referred them to *Nierembergia*. Soon after, Hemsley (1881) disagreed and related the name *Bouchetia procumbens* to a different series of Mexican plants. He noted that in *Bouchetia* the corolla tube tapers gradually and the stamens are free, inserted low in the corolla. Robinson (1904) reviewed some of the specimens cited by Hemsley and refused to accept them as the same species as plate 920. In this paper he described *Bouchetia arniatera* based on material cited by Hemsley and new material he had seen. Both Hemsley and Robinson based their concepts of *Bouchetia procumbens* on the Calques des Dessins copy of plate 920 and not on the copy in Geneva. Although agreeing in most details, the tracing copy differs notably from the Geneva copy in its poor rendition of flower buds which in this case are diagnostic.

With more material at hand and a view of both extant copies of plate 920, I must concur with Hooker and Robinson and relate *B. procumbens* to *Nierembergia* and not to *Bouchetia* as typified by *B. erecta*. *Nierembergia angustifolia* H.B.K. grows in Mexico and agrees with the plate in most features, especially in the following: leaves narrow, slightly broader above the middle, the flowers distributed along the branches rather than mostly terminal (as in *Bouchetia*), the calyx divided halfway or more with the lobes pointed and spreading, the corolla tube remaining narrow until well out of the tube, and pointed corolla lobes. The detailed drawings on plate 920 show 5 stamens inserted just above the top of the tube. And most important, the corolla buds (see Fig. 4B) consist of a slender, exserted tube with the unexpanded limb forming a subglobose or elliptic knob whereas in *Bouchetia* the exposed portion of the corolla in bud consists of a narrowly elliptic truncate limb, and the narrow portion of the tube is concealed by the calyx. The type of *Bouchetia procumbens* is the Geneva copy of Moçino & Sessé plate 920 which is a representation of *Nierembergia angustifolia* H.B.K. It is of interest that a collection of *Nierembergia angustifolia* is among the specimens from the Sessé & Moçino herbarium now at the Field Museum, Chicago.

The full citation for these names is *Bouchetia* DC. ex Dunal in DC. But to follow common practice, this may be shortened to *Bouchetia* Dunal in DC., or to *Bouchetia* Dun.

9a. **Salpiglossis anomala** (Miers) D'Arcy, comb. nov.

Nierembergia anomala Miers, London J. Bot. 5: 175. 1846. TYPE: Argentina, Cordoba, *Miers* (K).

?*N. staticifolia* Sendt. in Mart., Fl. Bras. 10: 179. 1 July 1846. TYPE: Brasil, *Sello* (B, if extant, not seen; photos C, MO).

Bouchetia anomala (Miers) Loes., Bot. Jahrb. Syst. 29: 105. 1901.

B. anomala (Miers) Britt. & Rusby, Trans. New York Acad. Sci. 7: 12. 1887, redundant combination.
?*B. anomala* subsp. *staticifolia* (Sendt.) Loes., Bot. Jahrb. Syst. 29: 106. 1900.
Nierembergia miersiana Sendt. in Mart., Fl. Bras. 10(1): 200 in obs. nomen nudum.
?*Petunia staticifolia* (Sendt.) O. Kuntze, Rev. Gen. Pl. 3(2): 223. 1898, in syn.
?*Nicotiana staticifolia* (Sendt.) O. Kuntze, Rev. Gen. Pl. 3(2): 223. 1898.

The photograph of the Sello collection which supports *Nierembergia staticifolia* appears to represent the same species as *Nierembergia anomala*, but it must be remembered that the synonymy effected here is based only on the photograph and a limited range of Argentinian material.

Salpiglossis anomala is quite similar to plants of North America treated here as *S. erecta*, but the pubescence is glandular and the calyx displays a more membranous area in the sinuses than the North American plants.

ARGENTINA. CHACO: *Schulz 7423* (C). CÓRDOBA: *Lossen 224* (F, MO); *Tweedie 1122* (K). CORRIENTES: *Pedersen 849, 9269* (both C). ENTRE RÍOS: *Huidobro 3474* (MO), *3426* (G). FORMOSA: *Jörgensen 2991* (MO); *Morel 5* (G); *Pederson 1268* (C). MISSIONES: Posadas, *Ekman 863* (G). SALTA: *Romero* 21 Jan. 1947 (C). TUCUMÁN: El Puestito, *Venturi 7355* (MO).

9b. **Salpiglossis arniatera** (Robinson) D'Arcy, comb. nov.—FIG. 5B.

Bouchetia arniatera Robinson, Bot. Gaz. (Crawfordsville) 38: 377. 1904. TYPE: Mexico, *Dugès* (GH, not seen; K, MINN, isotypes).

This species differs from the other Mexican species, *S. erecta*, in having a much longer corolla tube, which while it expands is still quite narrow until well beyond the calyx lobes. This corolla, apparently definitely purplish, is 2–3 cm long and opens to nearly 2 cm across. The calyx is larger than that of *S. erecta* and is proportionally more deeply lobed than other species of *Salpiglossis*. The plants are diminutive, less than 10 cm long, several stems arising from a woody rootstock.

Salpiglossis arniatera has been collected from widely scattered points in Mexico, mainly from the uplands. Its range is generally to the south and west of *S. erecta*. Across its range, the species shows some variation but this is difficult to ascertain from the few specimens available. It was first brought to scientific attention because it was reputed to poison sheep.

MEXICO. COAHUILA: 24 km NW of Fraile, 2350 m, *Stanford et al. 432* (MO). DISTRITO FEDERAL: Lomas, *Lyonnet 660* (K, MO). DURANGO: Vicinity of Rancho Ojito, *Correll & Johnston 21466* (TEX). MICHOACÁN: W of Morelia, *Gregg 787* (MO). NUEVO LEÓN: Cieneguillas to Pablillo, *Mueller & Mueller 870* (F, TEX). Hacienda Pabillo, Galeana, *Taylor 18* (F, MO), *74* (F, K, TEX). SAN LUIS POTOSÍ: Region of San Luis Potosí, *Parry & Palmer 701* (K, MO, US); *Schattner 1826* (K). TAMAULIPAS: *Stanford et al. 2603* (GH). VERACRUZ: Jalapa, *Graham 270* (K). ZACATECAS: Hacienda de Santiago, *Dugès 1904* (K, MINN).

9c. **Salpiglossis erecta** (Dun.) D'Arcy, comb. nov.—FIGS. 1E, 5A.

Bouchetia erecta DC. ex Dun. in DC., Prodr. 13(1): 589. 1582, based on Moçino & Sessé plate 921 (G).
Maleolaria lanceolata DC. ex Dun. in DC., Prodr. 13(1): 589. 1852, in syn. nom. nud. TYPE: *Pavón* (G).
Leucantha roemeriana Scheele, Linnaea 25: 259. 1852 (1853). TYPE: Texas, *Roemer* (B).
Nierembergia anomala var. *uniflora* Dun. in DC., Prodr. 13(1): 588. 1852. LECTOTYPE: Texas, *Drummond 245* (G-DC).
Bouchetia anomala sensu Britt. & Rusby, Trans. New York Acad. Sci. 7: 12. 1887, non Miers.
Bouchetia anomala subsp. *erecta* (DC.) Loes., Bot. Jahrb. Syst. 29: 105. 1900.

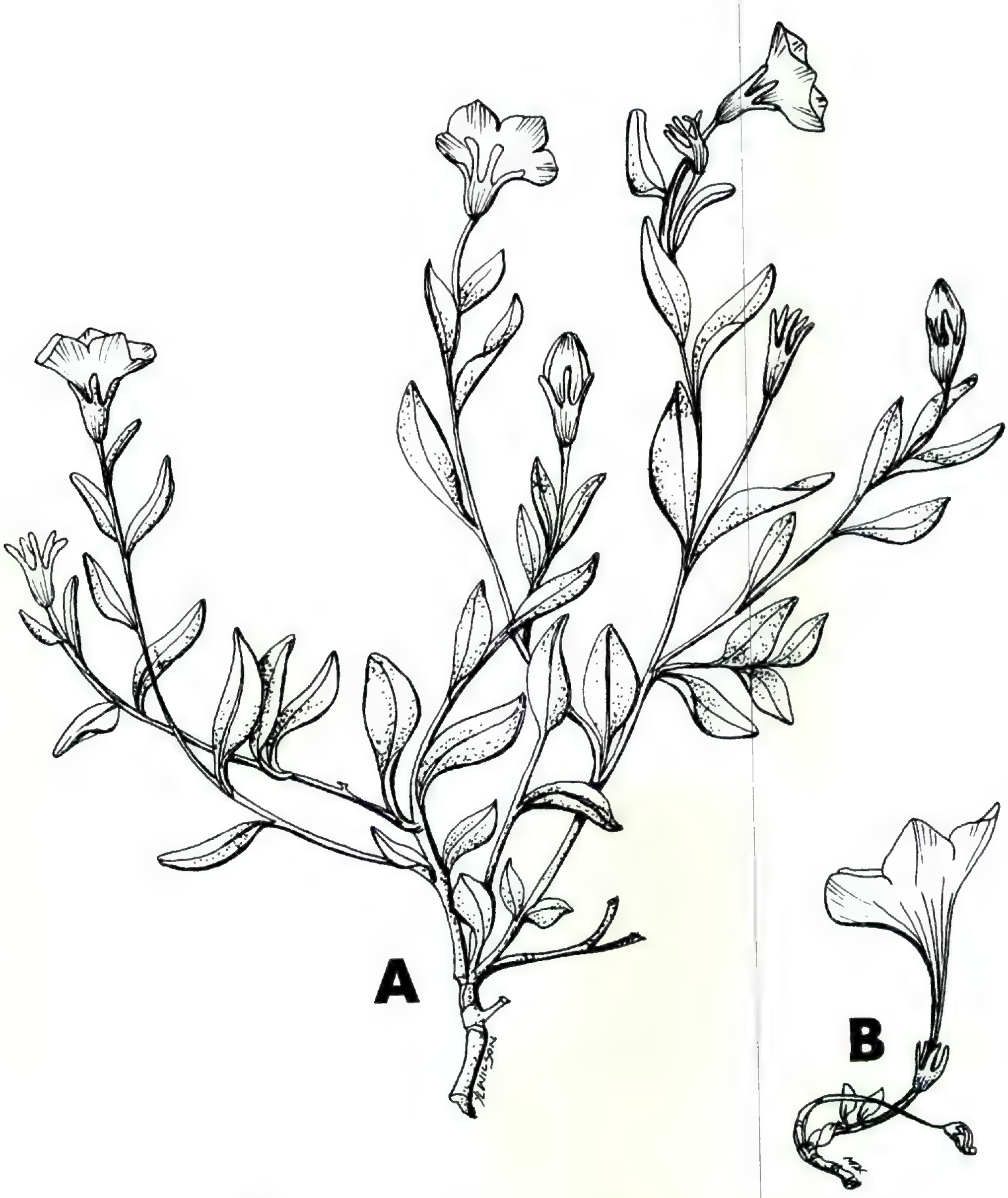

FIGURE 5. *Salpiglossis*.—A. *S. erecta* (Dun.) D'Arcy. Habit (×9/10). [After *Palmer 12124* (MO).]—B. *S. arniatera* (Robinson) D'Arcy. Flower (×1⅖). [After *Parry & Palmer 701* (MO).]

Diminutive *perennial* from a woody root, to 20 cm tall; stems flexuous, pubescent with short, white, appressed ascending hairs. *Leaves* elliptical, often narrowly so, mostly slightly wider above the middle, mostly 10–20 mm long, 4–7 mm wide, apically acute, sometimes minutely callose, costate, the lateral venation obscure, both sides minutely pubescent with appressed hairs, more so beneath; petiole to 5 mm long or obsolete. *Inflorescences* solitary or paired terminal flowers; pedicels to 3 cm long, subtended by normal leaves. *Flowers* with the calyx campanulate, 7–12 mm long, lobed ca. ¼ way down, the lobes

narrow, blunt, the tube 10-nerved, the sinus areas little differentiated, not accrescent; corolla mostly white, funnelform, to ca. 20 mm long, the tube included in the calyx, the limb campanulate to obconical, mostly exserted, becoming 10 mm across, shallowly lobed; stamens 4–5, one or more anther thecae sometimes reduced, inserted in the bottom half of the corolla tube; stigma 2-armed, slightly exceeding the anthers. *Capsule* 4-valved, slightly emergent from the calyx tube; seeds numerous, minute, prismatic.

Salpiglossis erecta ranges from Texas to Guatemala (Gentry & Standley, 1974). It has been collected from a wide range of open habitats. This species may not be distinct from *S. anomala* of Argentina, in which case the name *S. anomala* should be applied to the North American plants. There do appear to be differences between plants on the two continents, and careful study will be needed to assess the importance of these differences. *Salpiglossis erecta* was illustrated (as *Bouchetia*) by Gentry & Standley (1974).

UNITED STATES. TEXAS: San Antonio, *Bush 1184* (MO); *Clemens & Clemens 251* (F, MO), *249* (MO). 1½ mi NE of Vidauri, Refugio Co., *Correll 14822* (TEX). 9 mi W of Tivoli, Refugio Co., *Correll 27015* (TEX). 7.5 mi W of D'Hanis, Medina Co., *Correll & Rollins 32521* (TEX). 4 mi S of Marble Falls, Burnet Co., *Correll et al. 15902* (TEX). Seadrift, Calhoun Co., *Cory 49074* (TEX). San Filipo, *Drummond 245* (G, K). Near San Antonio, *Eggert* 4 April 1905 (MO). Near Bracken, *Groth 81* (F). Austin, *Hall 383* (F, MO). San Antonio, *Havard 12* (F). Gillespie Co., herb. Gustav *Jeremy* (MO). 13 mi N of San Antonio, Becar Co., *Johnston 2389* (TEX). 4.2 mi from Travis Co. line on Highway 183, Williamson Co., *Johnston & McCart 5256* (TEX). 5 mi S of Blanco, Blanco Co., *Johnston & Webster 509* (TEX). Without other locality, *Lindheimer 471 (276)* (F, K, MO). Comanche Springs, *Lindheimer 1034 (189)* (BM, C, G, MO, TEX). New Braunfels, *Lindheimer 1035 (346)* (C, F, K, M, MO, TEX). Without other locality, *Neally 1893* (MO). Uvalde, *Palmer 11041* (MO). Sabinal, *Palmer 11518* (MO). San Marcos, *Palmer 12124* (MO). Near San Saba, *Reverchon 1567* (F, MO). Yorktown, *Riedel 1942* (MO). 4 mi NW of Sinton, San Patricio Co., *Rogers 6648* (TEX). Harthaven, Travis Co., *Warnock W1007* (TEX). New Braunfels, Comal Co., *Warnock 46257* (TEX). Zilker Park, Travis Co., *Webster 61* (TEX). Without other locality, *Wright* (G-DC, left-hand specimen, MPU). Travis University Campus, Austin, *Young 1913* (MO, TEX).

MEXICO. COAHUILA: Lerios, 10,000 ft, *Palmer 852* (F). HIDALGO: Near Jacala, *Edwards 763* (F). Hills above Pachuca, 8500 ft, *Pringle* (BM, F, G, K, MO, MSC). MÉXICO: 20 km NE of Texcoco, 2850 m, *Cisneros* (MSC). 5 km N of Atizapán, 2350 m, *Rzedowski 20881* (MSC). MICHOACÁN: Near Morelia, *Arsène 5595* (MO). MORELIA: Punguato, *Arsène 52b* (F). NUEVO LEÓN: 12 mi E of Monterrey, *Barkley 14368* (TEX). Nuevo León, *Lacas 325* (F). Santiago, 2300 ft, *Leavenworth 124* (F). 18 km S of Monterrey, *Marroguin 1339* (TEX). Monterrey, *Mueller & Mueller 290* (TEX). 15 mi SW of Pueblo Galeana, 7500–8000 ft, *Mueller & Mueller 334* (TEX). Road up Chipinque, *Webster & Aquirre 2951* (TEX). PUEBLA: Esperanza, *Purpus 2494* (BM, F, G, MO). Near San Luis Tultitlanapa, *Purpus 3265* (MO). SAN LUIS POTOSÍ: 30 mi E of San Luis Potosí, 6900 ft, *McGregor et al. 577* (TEX). Minas de San Rafael, *Purpus 5350* (F, MO).

9d. **Salpiglossis sinuata** Ruiz & Pavón, Syst. Veg. 163. 1798. TYPE: Peru, *Ruiz*, not seen.

S. straminea Hook., Exot. Fl. 3, *tab.* 229. 1823.

S. picta Sweet, Brit. Flower Gard., ser. 1, *tab.* 258. 1826.

S. atro-purpurea R. Graham, Edinburgh New Philos. J. 1827 (Oct.–Dec.): 176. 1827. TYPE: not seen. Based on plants cultivated in Scotland from seed received from Gillies, collected on hills 50 mi beyond (W of) Mendoza.

S. intermedia Sweet, Hort. Brit., ed. 2: 594. 1830; Brit. Flower Gard., ser. 2, *tab. 112.* 1831. Based on a plant cultivated in England.

S. barclayana Sweet, Brit. Flower Gard., ser. 2, *tab. 112.* 1833. Based on a plant cultivated in England.

S. barcklayana Penny ex G. Don., Loud, Hort. Brit. Suppl. 1: 599. 1850 (not seen).

S. *coccinea* Lindl. & Paxt., Flow. Gard. 3: 135, *tab. 100.* 1852–1853.
S. *aurea* Hort. ex Vilm., Fl. Pl. Terre, ed. 1: 762. 1863 (not seen).
S. *hybrida* Vilm., Fl. Pl. Terre, ed. 1: 767. 1863 (not seen).
S. *variabilis* Vilm., Fl. Pl. Terre, ed. 2: 809. 1866 (not seen), nom. nud. Based on a plant cultivated in France.

This species is widely cultivated in north temperate gardens. This and *S. spinescens* are the only large-flowered species in the genus. It is quite variable in flower color suggesting more than one taxonomic element may be present.

CHILE. Cordilleras, *Cuming's Herb. 246, 294, 371, 445* (all GH). Without other locality, *Gay 204* (GH, NY). Pajo Cruz, 1500 m, *Kuntze 192* (NY). Andes, Capt. *Reynolds* (GH). ACONAGUA: 3 km E of Río Blanco, 1700 m, *Hutchinson 175* (GH). Ca. 15 km E of Melón, 1700 m, *Morrison 16856* (GH, MO). 18 km E of La Ligua, 1900–2200 m, *Morrison 17067* (MO). Riecillo, 1400 m, *Zöllner 8391* (MO). COLCHAGUA: Near Quinta and Taguatagua, *Bertero 1289* (?599) (NY). Centinela, San Fernando, *Montero 20* (GH). CURICÓ: Los Quenes, Andes de Curicó, 1000 m, *Aravena 33374* (GH, MO). Hacienda Monte Grande, 1600 m, *Werdermann 506* (GH, MO, NY). MALLECO: Ercilla, *Kuntze II 192* (NY). MAULE: Near Cauguenes, *Reid* (NY). O'HIGGINS: Copada, *Pennell 12236* (NY). SANTIAGO: Prope Tiltil, 1400 m, *Grandjot x31, x32* (both MO). Cerro Provincia, Cordillera de Santiago, 1600 m, *Grandjot xi1932, 3637* (GH). Santiago, 1400 m, *Montero 312* (GH, MO). Cumbra de la Dormida, *Senn 4527* (MO). VALPARAÍSO: Valparaíso, *Bertero 1290* (NY). Concón, *Miers* (MO). Las Viscachas, 10 km from La Dormida, 1700–1900 m, *Morrison 16747* (GH). Ca. 12 km from Valparaíso, 50–60 m, *Morrison 16835* (GH, MO). Prope Concón, *Poeppig 163* (GH, MO).

PERU. Perou, *Dombey* (NY).

9e. **Salpiglossis spinescens** Clos in Gay, Fl. Chil. 5: 127. 1849. TYPE: Chile, Copaipo, *Gay* Feb. 1843 (G, not seen; photo MO).

This is a large flowered species with corollas to 4 cm long. The plants are densely glandular-pilose and some shoots are indurated into spinelike processes. A shrub approaching a meter in stature, the stems are devoid of normally developed leaves. Clos reported that it occurs in Coquimbo as well as in Atacamá. Werdermann (1928) found it only in Copaipo.

CHILE. ATACAMÁ: Desert of Atacamá, *Geisse 16* (NY). Below Agua Dulce, Quebrada de Potrerillos, 2500 m, *Johnston 3683* (GH). Tierra amarilla, dept. Copaipo, 700 m, *Werdermann 419* (GH, MO, NY).

EXCLUDED NAMES

A number of names published in *Salpiglossis* have been noted under other genera in this paper. Several names must be excluded:

Salpiglossis fulva Court., Amer. Gard. Mag. 1: 219, n. 411. 1835.
S. *integrifolia* Lodd., Bot. Cab. *tab. 1978.* 1833. = *Petunia* sp. TYPE: Cultivated in Scotland from seed received from Buenos Aires (not seen).
S. *integrifolia* Hook., Bot. Mag. *tab. 3113.* 1831. = ?*Petunia violacea* Lindl.

Petunia integrifolia (Hook.) Schinz & Thell., Vierteljahrschr. Naturf. Ges. Zürich 60: 361. 1915; *Nicotiana integrifolia* (Hook.) O. Kuntze.

S. *linearis* Hook., Bot. Mag. sub *tab. 3113.* 1831. = *Petunia linearis* (Hook.) Paxt.
S. *parviflora* G. Don. ex Benth. in DC., Prodr. 10: 202. 1846, nom. nud. = ?
S. *prostrata* Hook. & Arn., Bot. Beech Voy. 153. 1841. = *Petunia parviflora* Juss., fide Fries 1911. TYPE: California (?K, not seen).
S. *purpurea* Miers, Trav. 2: 531. 1826, nom. nud.

S. sinuata Hook. & Arn. ex Miers, London J. Bot. 5: 190. 1846, nom. nud., non Ruiz & Pavón = *Petunia parviflora* Juss., fide Fries 1911.

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STUDIES IN BIGNONIACEAE 31: NEW SPECIES AND COMBINATIONS FROM AMAZONIAN PERU AND BRAZIL[1]

ALWYN H. GENTRY[2]

ABSTRACT

Recent collections of Bignoniaceae from Amazonian Peru and Brazil include six undescribed species—*Adenocalymma prancei* A. Gentry, *Arrabidaea revillae* A. Gentry, *Distictella reticulata* A. Gentry, *Jacaranda bullata* A. Gentry, *Memora racemosa* A. Gentry, and *Tabebuia incana* A. Gentry. A new combination for another species of Amazonian Bignoniaceae—*Manaosella cordifolia* (DC.) A. Gentry—is also proposed.

Adenocalymma prancei A. Gentry, sp. nov.

Frutex scandens, ramulis teretibus, glabrescentibus. Folia 2-foliolata, foliolis anguste ellipticis plus minusve glabrescentibus. Inflorescentia racemosa, axillaris, puberula; calyx cupulatus, 5-denticulatus, puberulus; corolla aurea, tubulo-campanulata, extus puberula; ovarium cylindricum, glabrum. Capsula lineari-oblonga, minute puberula.

Liana; branchlets terete, when young minutely puberulous with simple and forked whitish trichomes, glabrescent, the nodes without interpetiolar glandular fields; pseudostipules thick-foliaceous, linear-oblong, 5–13 mm long. Leaves 2-foliolate, sometimes with a simple tendril; leaflets elliptic or narrowly elliptic to lanceolate-elliptic, rounded to cuneate at the base, 10–21 cm long, 3–10 cm wide, subcoriaceous, the veins and veinlets prominulous below, glabrous or glabrescent above, more or less glabrescent below, when young with scattered minute simple and forked trichomes, especially along the main veins, drying olive; petiolule 1–3 cm long; petiole 1–2.5 cm long, glabrate or minutely puberulous with simple and forked trichomes. Inflorescence an axillary raceme, puberulous with simple and forked trichomes; bracts small, 2–3 mm long, ovate, densely puberulous, early caducous; bracteoles small, ca. 2 mm long, ovate, early caducous. Flowers with the calyx cupular, shallowly 5-dentate or 5-denticulate (sometimes spathaceously split) (7–)8–10 mm long, 6–7 mm wide, puberulous, with raised glands near the margin; corolla yellow, tubular-campanulate above a somewhat narrowed base, 4.5–7 cm long, ca. 1 cm wide at the mouth of the tube, the tube 3.5–5 cm long, the lobes 1–1.8 cm long, puberulous outside with simple and stellate trichomes, the lobes inside glandular-lepidote and slightly scattered puberulous, the tube glabrous inside except at and below the base of the stamens; stamens didynamous, inserted 12–13 mm above the base of the tube, the anther thecae divaricate, 3 mm long, the filaments 1.5–2.5 cm long; pistil 3.5–5 cm long, the ovary linear-cylindric, 3 mm long, 1 mm wide, glabrous; disc patelliform 0.5 mm long, 2 mm wide. Capsule (immature) com-

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[1] My studies of Amazonian plants have been supported by NSF grants GB-40103 and DEB 75-20325.

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ANN. MISSOURI BOT. GARD. 65: 725–735. 1978.

0026-6493/78/0725–0735/$01.15/0

pressed, linear-oblong, 9 cm long, to 1.2 cm wide, minutely whitish puberulous with simple trichomes, also with scattered dark-drying glands.

TYPE: BRAZIL. AMAZONAS: 3–6 km N of Manaus-Itacoatiara Road near Rio Preto da Eva (Km 79), vine, flowers yellow, 3 Dec. 1974, *Gentry & Ramos 13063* (INPA, holotype; MO, MG, NY, isotypes).

Additional collections examined: BRAZIL. AMAZONAS: Estrado do Aleixo near Manaus, 6–7 km past INPA, sterile vine, 2 Dec. 1974, *Gentry 13037* (INPA, MO). 2–5 km N of Manaus-Itacoatiara Road at Km 79 near Rio Preto da Eva, 100–200 m, sterile vine, 24 Nov. 1974, *Gentry 12830* (INPA, MO). Ducke Forest Reserve, Km 26 on the Manaus-Itacoatiara Road, sterile vine, 23 Nov. 1974, *Gentry 12818* (INPA, MO). INPA Campus, Manaus, sterile vine, 30 Nov. 1974, *Gentry 13015* (INPA, MO). Rio Cuieras, 2 km below mouth of Rio Brancinho, liana, corolla yellow, 11 Sep. 1973, *Prance et al. 17778* (INPA, MO, NY). Rio Purus, Rio Ituxi, Lago Preto, 2 km N of Lábrea, 5 cm wide, flowers lemon yellow, 26 June 1971, *Prance et al. 13758* (NY).

FRENCH GUIANA: Fleuve Maroni entre Kaiapou et Papaichton, liane ripicole, pétalos jaunes, fruits verts, 28 Apr. 1975, *Sastre et al. 4011* (MO).

PERU. HUANUCO: Tingo Maria, 780–900 m, sterile vine, leaves whitish beneath, 28 Mar. 1977, *Gentry & Daly 18783* (MO).

I have previously considered this a glabrescent-leaved variant of *A. subincanum* Hub. However, discovery of fruiting specimens of both species makes lumping untenable—*A. subincanum* has short, thick, densely tannish-dendroid-pubescent fruits and thick wingless seeds. The calyx of *A. prancei* is also longer than that of *A. subincanum* [(7–)8–9(–10) mm versus 5–6 mm] and it has simple and forked, rather than stellate, vegetative trichomes and is often completely glabrescent. The ranges of the two species are apparently distinct as well, with *A. prancei* in central and upper Amazonia (north to French Guiana) and *A. subincanum* in lower Amazonia from Itacoatiara to the Rio Jarí and southeast to northern Maranhão State.

Another close relative of *A. prancei* is *A. apparicianum* J. C. Gom. of Ceará, Brazil, which has a longer calyx (12–15 mm), wider fruit (2–2.5 cm), and leaflets smaller and noticeably simple-puberulous beneath.

It is possible that the Rio Purus collection, which consists of only three buds and four leaflets, is not this species. Its leaflets are larger (20–25 by 10–12 cm) and more coriaceous and bullate than described above for *A. prancei.*

Arrabidaea revillae A. Gentry, sp. nov.—FIG. 1.

Frutex scandens, ramulis teretibus, glabris. Folia 2–3-foliolata, foliolis ovatis vel ovato-ellipticis, subtus nervorum lateralium in axillibus barbatis. Inflorescentia axillaris, plerumque racemosa, pauciflora, lepidota et sparsim puberula; calyx tubulosus, bilabiatus vel calyptratus et truncatus, sparsim lepidotus puberulusque; corolla rosea, tubulo-infundibuliformis, extus puberula; ovarium oblongum, dense lepidotum. Capsula lineari-oblonga, complanata, sparsim lepidota, seminibus sin alis.

Liana; branchlets terete with widely spaced pale raised lenticels, glabrous, longitudinally striate, without interpetiolar glandular fields; pseudostipules not evident. Leaves 3-foliolate or 2-foliolate with a simple tendril or tendril scar; leaflets ovate to ovate-elliptic, rounded at the base, acute to very shortly acuminate at the apex, 7–15 cm long, 4–8.5 cm wide, chartaceous, above minutely puberulous along the midvein, otherwise glabrous, below conspicuously barbate in the axils of the lateral nerves, otherwise glabrous except for scattered minute

FIGURE 1. *Arrabidaea revillae* A. Gentry.—A. Leaves (×½). [After *Revilla 737* (MO)].—B. Fruit and seed (×½). [After *Rimachi 787* (MO)].—C. Inflorescence (×½). [After *Revilla 737* (MO)].

reddish lepidote scales; petiolules 1–3.5 cm long; petiole 2.5–7 cm long, minutely puberulous and scattered reddish lepidote. Inflorescence axillary, more or less paniculate but usually strongly contracted and more or less racemose, lepidote and sparsely puberulous, drying blackish; bracts and bracteoles linear, to 2 mm long; buds narrow and pointed. Flowers with the calyx tubular, irreg-

ularly bilabiate or calypterate and subtruncate, 10–14 mm long, 5–8 mm wide, very sparsely puberulous and lepidote, drying blackish; corolla magenta, tubular-infundibuliform, 3.5–6 cm long, 0.6–1 cm wide at the mouth of the tube, the tube 3–4 cm long, the lobes 0.6–1.5 cm long, puberulous outside and on the lobes inside villous at the level of stamen insertion; stamens didynamous, inserted 10–12 mm from the base of the tube, the filaments 1.2–1.7 cm long, the anther thecae divaricate, 2 mm long, the connective slightly extended; pistil 2.8–3.2 cm long, the ovary oblong, somewhat flattened, densely lepidote, 2 mm long, 1 mm wide; disc annular-pulvinate, 1.5 mm long, 3 mm wide. Capsule linear-oblong, compressed, 20–27 cm long, 2.5–2.8 cm wide, the midrib not evident, drying blackish, scattered lepidote, the surface not gland-pitted; seeds 2.4–2.5 cm long, 3.6–3.9 cm wide, slightly thickened and corky, wingless.

TYPE: PERU. LORETO: Provincia Maynas, Distrito Pebas, Río Yahuasyacu, afluente del Río Ampiyacu, bejuco de la ribera, flores blancas y lilas, 18 June 1976, *Revilla 718* (MO, holotype; COL, F, NY, UNAP (Iquitos), USM, isotypes).

Additional collections examined: PERU. LORETO: Provincia Maynas, Quebrada de Uchpa Cano across the Río Itaya from Iquitos, fruits green, 25 Jan. 1974, *Rimachi 787* (MO). Río Amazonas, S of Iquitos, flowers reddish violet, 18 Aug. 1972, *Croat 19355* (MO). Isla de Ushpa-Cano near the mouth of the Río Itaya, flowers orchid, fruits green, 24 Aug. 1972, *Croat 19657* (MO). Mishayacu near Iquitos, 100 m, liana, flowers dark violet, Apr. 1930, *Klug 1228* (US). Distrito Pebas, Río Yahuasyacu, afluente del Río Ampiyacu, flores lilas, 18 June 1976, *Revilla 737* (F, MO, NY, INPA, UNAP (Iquitos), USM).
BRAZIL. AMAZONAS: Parana do Xiboremo, near Manaus, May 1953, *Fróes 29623* (IAN).

This species is closely related to the widespread and variable *A. corallina* (Jacq.) Sandw. which is apparently absent in upper Amazonia. The most striking difference between *A. revillae* and *A. corallina* is the former's wingless, presumably water-dispersed seeds. The fruit of *A. revillae* is also wider than that of *A. corallina* (which is less than 2.3 cm wide), dries black rather than tan or brownish, and does not have a glandular-pitted surface. The corolla is narrower than in *A. corallina* and tubular-infundibuliform rather than tubular-campanulate. Other differences from *A. corallina* include a usually much more contracted inflorescence, narrowly pointed buds, longer calyx (when not calypterate), and the characteristic grayish color of the dried leaves.

Distictella reticulata A. Gentry, sp. nov.

Frutex scandens, ramulis teretibus, villoso-tomentosis. Folia 2–3-foliolata, foliolis ellipticis vel ovatis, nervatura supra impressa, subtus prominenti valde reticulata areolis puberulis. Inflorescentia racemosa, terminalis, puberula; calyx cupulatus, truncatus, puberulus; corolla alba, extus dense puberula; ovarium oblongum, puberulum. Capsula elliptica, villoso-tomentosa.

Liana; brachlets terete, villous-tomentose, the nodes without interpetiolar glandular fields or pseudostipules. Leaves 2–3-foliolate, sometimes with a trifid tendril; leaflets elliptic to ovate, obtuse to rounded at the apex, rounded at the base, 5–11 cm long, 3–8 cm wide, coriaceous, all veins and veinlets more or less impressed above and strongly raised beneath, the lower surface thus intricately reticulate, glabrous or glabrescent above except for occasional trichomes at the base of the midvein, below pilose-tomentose, especially within the areoles, drying brownish olive above and below; petiolules 0.5–1 cm long; petiole 1–1.3 cm

long, tomentose. Inflorescence a terminal raceme or racemiform with the lower pedicels converted into 2- or 3-flowered peduncles, brownish tomentose; bracts and bracteoles caducous. Flowers with the calyx cupular, circumscissile at the base in fruit, truncate, 10–14 mm long, 10–12 mm wide, densely appressed-puberulous with tannish simple trichomes, with or without plate-shaped glands; corolla white, thickish, tubular-campanulate above a narrowed base, strongly bent above the base, 4.5–6.5 cm long, 1.5–2.5 cm wide at the mouth of the tube, the tube 3–4.5 cm long, the lobes 1.5–2 cm long, densely puberulous outside, the lobes glandular-lepidote inside, slightly glandular villous at the level of stamen insertion; stamens didynamous, inserted ca. 12 mm above the base of the tube, the anther thecae divaricate, ca. 4 mm long; ovary oblong, 4-grooved, 4 mm long, 2 mm wide, densely appressed puberulous; disc conical, 2 mm long, 4 mm wide. Capsule elliptic, somewhat compressed, the valves thick and woody, the midrib not visible, 6 cm long, 2.8 cm wide, softly villous-tomentose with erect reddish brown trichomes; seeds thin, rather asymmetrically bialate, ca. 1.5 cm long and 3.5 cm wide, the wings brown, membranous, not distinctly demarcated from the seed body.

TYPE: BRAZIL. AMAZONAS: Manaus, Igarapé de Cachoeira Alta do Tarumã, terreno arenoso, capoeira, trepadeira com gavinhas, frutos ainda verdes, 28 Aug. 1962, *Rodrigues & Chagas 4610* (INPA, holotype; MO, isotype).

Additional collections examined: BRAZIL. AMAZONAS: Manaus, Flores, igapó do riacho, cipó, fl. branca, 30 June 1941, *Ducke s.n.* (*RB-53243*) (RB). Manaus, margem do igrapé da cachoeira Alta, estrada da Forquilha, 24 Aug. 1955, *Chagas 1705* (K). Manaus, margem do igarapé do Parque 10, 27 July 1956, *Chagas 3994* (K). Manaus, margem do igarapé da cachoeira Alta do Tarumã, flores alvas, 6 July 1955, *Chagas 1330* (K), 30 May 1955, *Chagas 1086* (K). Manaus, flores alvas, estames róseas, 25 June 1956, *Francisco & Dionisio 3940* (K).

The leaflets of this species are very like the simple leaves of *D. monophylla* Sandw. of the Guayana region in their strikingly sculptured reticulum but are otherwise unique in the genus. Besides having subsessile simple leaves, *D. monophylla* is a subshrub with few-flowered inflorescences, smaller calyces, and gland-dotted fruits. Among viny species, *D. reticulata* may be compared with *D. dasytricha* Sandw. of southcentral and southwestern Brazil, which has a much longer shaggy indumentum, and *D. obovata* Sandw. of the Guayana highlands, which has smaller, differently shaped leaves, smaller calyces, and warty-lenticellate fruits.

Jacaranda bullata A. Gentry, sp. nov.—FIG. 2.

Folia pinnatim composita, 11–17-foliolata, foliolis acutis, subsessilibus, 2–7 cm longis, 0.6–2.3 cm latis. Inflorescentia anguste paniculata, fere racemosa; calyx campanulatus, minute 5-denticulatus; corolla anguste tubulo-campanulata, extus puberula; antherae 2-thecatae; ovarium glabrum. Fructus ellipticus, complanatus, seminibus alatis.

Branchlets subtetragonal, without noticeable lenticels. Leaves simply pinnate with 11–17 leaflets; leaflets asymmetrically elliptic or rhombic-elliptic, acutish at the apex, obtuse at the base, subsessile, membranous, 2–7 cm long, 0.6–2.3 cm wide, entire to remotely serrate, glabrous above, puberulous with short curved trichomes along the margin and the veins beneath, more or less bullate

FIGURE 2. *Jacaranda bullata* A. Gentry.—A. Habit (×⅜).—B. Flower (×⅜). [After *Froes & Addison 29141* (IAN)].

with all the veins impressed above and raised beneath. Inflorescence terminal, very narrowly paniculate, almost racemose, the lateral branches 2–3-flowered and mostly less than 1 cm long, puberulous. Flowers with the calyx campanulate, essentially truncate, minutely and evenly 5-denticulate, 5 mm long, 4 mm wide, sparsely lepidote, otherwise glabrous or with a few minute trichomes near the

margin; corolla pink ("rosea"), narrowly tubular-campanulate, 4 cm long, 0.8 cm wide at the mouth of the tube, the tube 3.5 cm long, the lobes 0.5 cm long, minutely stalked glandular-lepidote outside, conspicuously so in bud, very inconspicuously so at anthesis, the lobes puberulous outside and inside, especially toward the tips; stamens didynamous, the anther thecae divaricate, 2.5 mm long, the staminode ca. 2.8 cm long, capitate, glandular-villous for the middle 5 cm and the apical 6 cm, otherwise glandular-lepidote; ovary ovate, ca. 1.3 mm long and wide, glabrous; disk patelliform, ca. 0.5 mm long and 2.5 mm wide. Capsule elliptic, strongly compressed, subacute at the base and the apex, 3.7–5 cm long, 2.3–3 cm wide, glabrous except for a few scattered lepidote scales; seeds 0.7–1 cm long, 1.4–1.7 cm wide, the brown seed body almost surrounded by the thin brownish-hyaline wings.

TYPE: BRAZIL. AMAZONAS: Margem do Rio Aracá (Rio Negro drainage north of Barcelos), terra firme, alta, 29 Oct. 1952, *Fróes & Addison 29141* (IAN, holotype; K (2 sheets), US, MO fragment, isotypes).

Sandwith recognized this as a probable new species according to a note on the Kew material but refrained from describing it since the Kew duplicate had only a single shriveled corolla. The IAN duplicate selected as the holotype includes a single well-pressed corolla—the basis of the above floral description—which makes the description of this distinctive species possible. Its closest relative is probably the rarely collected *J. heteroptila* Bureau & K. Schum. of northeastern Brazil, which sometimes has once-pinnate leaves but fewer—not all bullate—leaflets, an openly paniculate—almost glabrous—inflorescence, bilabiate calyx, and larger (7 by 4.2 cm), more oblong fruit. A relationship with *Jacaranda egleri* Sandw. of the Rio Tapajos region might also be suggested, but that species differs especially in its much smaller, more coriaceous, nonbullate leaflets and also in a slender, few-flowered, glabrescent inflorescence, campanulate, 5-dentate calyx, smaller corolla with a long basal constriction, and smaller capsule.

Memora racemosa A. Gentry, sp. nov.

Frutex scandens, ramulis teretibus, glabris. Folia 2-foliolata vel pinnatim 5–7-foliolata, foliolis ovatis, subtus minute puberulis. Inflorescentia racemosa elongata, axillaris, minute lepidota, bractis bracteolisque parvulis, caducis; calyx campanulatus, minute 5-denticulatus; corolla flava, tubulo-infundibuliformis, extus glabra; ovarium lineare, minute lepidotum. Capsula linearis, valde complanata, aliquantum lepidota.

Liana; branchlets terete, glabrous, drying dark with numerous minute roundish lenticels, the nodes without interpetiolar glandular fields; pseudostipules small, blunt, subwoody, ca. 2 mm long. Leaves 2-foliolate (mostly) to simply pinnate with up to 7 leaflets, 2-foliolate leaves often with a simple tendril; leaflets ovate to elliptic-ovate, obtuse to acuminate, rounded to cuneate at the base, subcoriaceous, 7–14 cm long, 3–6 cm wide, minutely appressed puberulous and papillose-puberulous below, glabrous above except for a few minute trichomes at the base of the midvein; petiolules and petiole inconspicuously and minutely scattered-puberulous dorsally. Inflorescence an elongate axillary raceme, often several per node, rarely branched near the base with each branch racemose, drying dark, minutely lepidote; pedicels 8–16 mm long; bracts linear, 4–5 mm

long, 1 mm wide, caducous; bracteoles sublinear, ca. 4 mm long and 1 mm wide, usually near the middle of the pedicel. Flowers with the calyx campanulate, coriaceous, truncate, minutely 5-denticulate, 6–10 mm long, 6–9 mm wide, drying black, glandular, scattered-lepidote, otherwise glabrous or puberulous with a few appressed trichomes mostly near the apex; corolla yellow, tubular-infundibuliform, 4.5–6.5 cm long, 0.9–1.6 cm wide at the mouth of the tube, the tube 3.5–5 cm long, the lobes 1–1.5 cm long, glabrous outside and inside except for glandular trichomes at the level of stamen insertion; stamens didynamous, inserted ca. 10 mm from the base of the tube, the filaments 1.3–2 cm long, the thecae divaricate, 3 mm long; pistil 3–3.5 cm long, the ovary linear, 3–4 mm long, ca. 0.6 mm wide, minutely lepidote; disc patelliform-pulvinate, 1.5–2 mm long, 3 mm wide. Capsule (immature) linear, strongly compressed with slightly thicker margins, 25–40 cm long, to ca. 1.3 cm wide, drying black without a visible midline, reddish-lepidote, otherwise glabrous.

TYPE: BRAZIL. PARA: Km 93, Belém-Brasília Highway, liana on high tree, flowers yellow, frequent on high ground, 5 Aug. 1963. *Maguire et al. 56008* (MO-2232814, holotype; MO-2279292, COL, NY, isotypes).

Additional collections examined: BRAZIL. PARA: Rio Tocantins, Jacundá, terra firme, mata central, 15 May 1951, *Fróes 27107* (IAN). Km 249–254, Rodovia Belém-Brasília, cipó sobre árvore, flores amarelas, mata terra firme, beira da estrada, 7 July 1960, *Oliveira 873* (IAN). Km 289–293, Rodovia Belém-Brasília, 31 July 1960, *Oliveira 948* (IAN). MARANHÃO: Km 338, Rodovia Belém-Brasília, beira da estrada, 24 Aug. 1960, *Oliveira 1040* (IAN, 2 sheets).

SURINAM. Lely Mountains, 175 km SSE of Paramaribo, 500–700 m, NW corner of plateau no. 1, woody vine, corolla yellow, young twigs and inflorescence rachises sticky, 13 Oct. 1976, *Mori & Bolten 8467* (MO), western edge of plateau 2, woody vine, corolla yellow, 16 Oct. 1976, *Mori & Bolten 8512* (MO).

This species is related to *M. patula* Miers, from which it differs in the more open, elongate inflorescence with smaller bracts and bracteoles, and to *M. biternata* A. Samp., which has branching inflorescences, sessile or subsessile leaflets, and wider bracteoles just below the calyx. Both of these species have broader fruits than *M. racemosa*. *Memora racemosa* is unique in the genus in the minutely appressed puberulous leaf undersides, a feature somewhat reminiscent of *Arrabidaea candicans* (L. Rich.) DC.

Tabebuia incana A. Gentry, sp. nov.

Arbor ad 30 m altam. Folia palmatim 5-foliolata, foliolis ellipticis, integris, infra dense stellato-tomentosis trichomatibus adpressis, argenteis. Inflorescentia paniculata, congesta, ramis dense stellato-rufescentibus. Flores calyce campanulato, stellato-rufescenti; corolla lutea, extus glabra, intus fauce villosa, ovarium oblongum, glabrum. Capsula ignota.

Tree to 30 m; branchlets subtetragonal, the epidermis rather loose, minutely stellate-tomentose when young. Leaves palmately 5-foliolate; leaflets evenly elliptic, acute, rounded or broadly cuneate at the base, 3.5–12 cm long, 1.2–6 cm wide, entire, membranous to chartaceous, above stellate pubescent along the midvein, otherwise scattered lepidote, below densely tomentose with minute sessile or subsessile stellate trichomes, drying brown or blackish above, contrastingly tan or silvery below from the trichomes, the less pubescent veins below

drying darker; petiolules 0.5–2.7 cm long; petiole 3.5–8 cm long, finely stellate-tomentose. Inflorescence a highly contracted subfasciculate panicle; peduncles and pedicels hardly visible, less than 5 mm long, stellate rufescent. Flowers with the calyx campanulate, 5–8 mm long, 5–7 mm wide, densely stellate-rufescent, also with some simple trichomes; corolla yellow, tubular-infundibuliform, 6–7.2 cm long, ca. 1.5 cm wide at the mouth of the tube, the tube 4.8–5.5 cm long, the lobes 1.5–2 cm long, the tube glabrous outside, the lobes lepidote and ciliate, otherwise glabrous, the tube inside glabrous dorsally, densely villous with simple trichomes to 1.5 mm long ventrally, villous at the level of stamen insertion; stamens didynamous, the anther thecae divaricate, 2–3 mm long, the longer filaments 1.6–2 cm long, the shorter filaments 1.2–1.4 cm long, the staminode ca. 2 mm long, inserted 6–7 mm from the base of the corolla tube; pistil 2.4–2.5 cm long, the ovary oblong, 5 mm long, 1.5 mm wide, glabrous, finely longitudinally impressed-striate, the ovules ca. 8-seriate in each locule; disc pulvinate, 0.7 mm long, 2 mm wide. Capsule unknown.

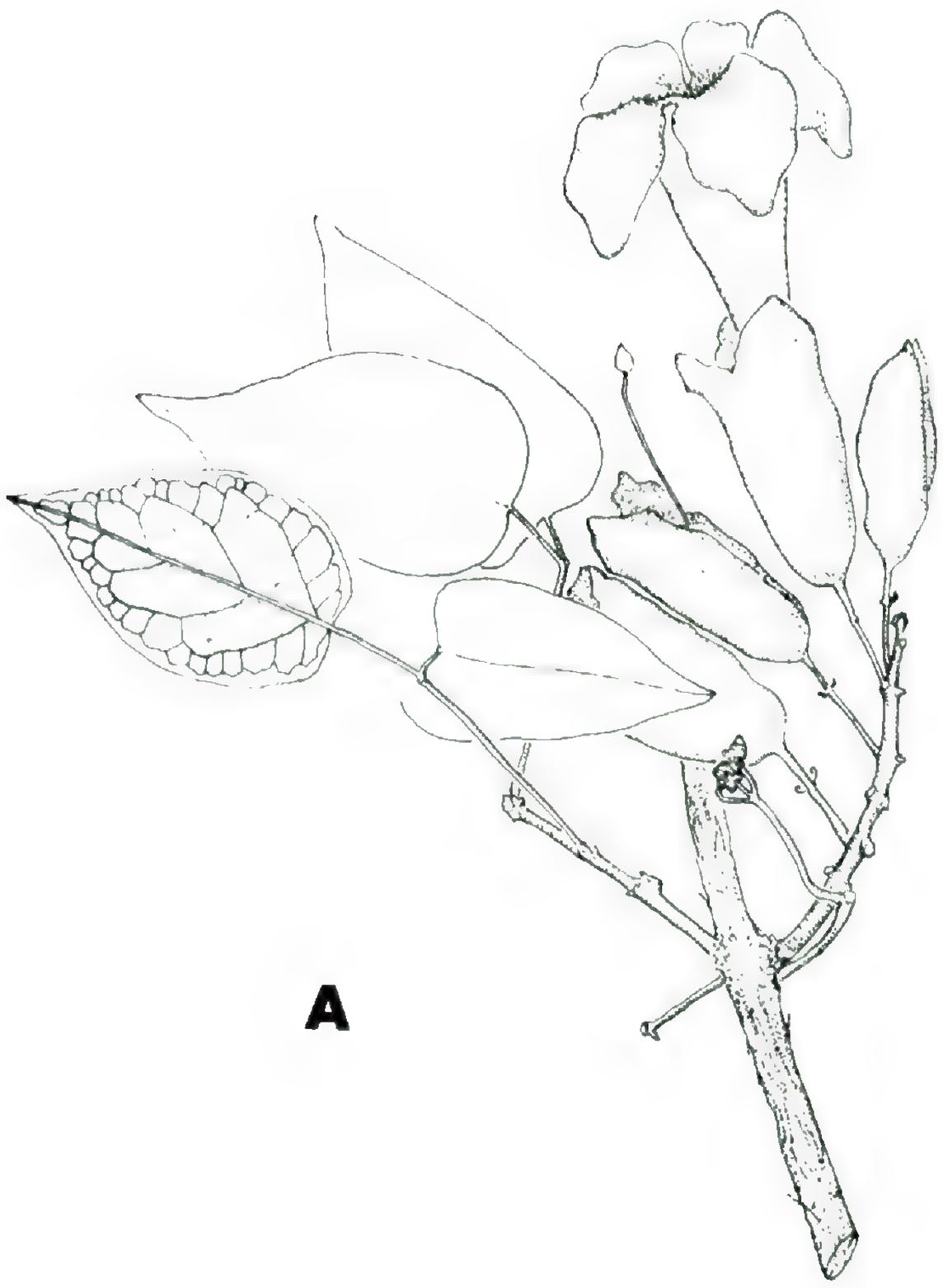
TYPE: BRAZIL. AMAZONAS: Manaus, Reserva Florestal Ducke, inventario florestal (Dr. William), árvore 2205, hectare 05D, fenológico 101, árvore de 30 m de altura por 30 cm de diâmetro, na mata de terra firme em solo argiloso, flores amarelas sem aroma, 29 Oct. 1968, *J. Aluisio 236* (INPA-23866) (INPA, holotype; MO, isotype).

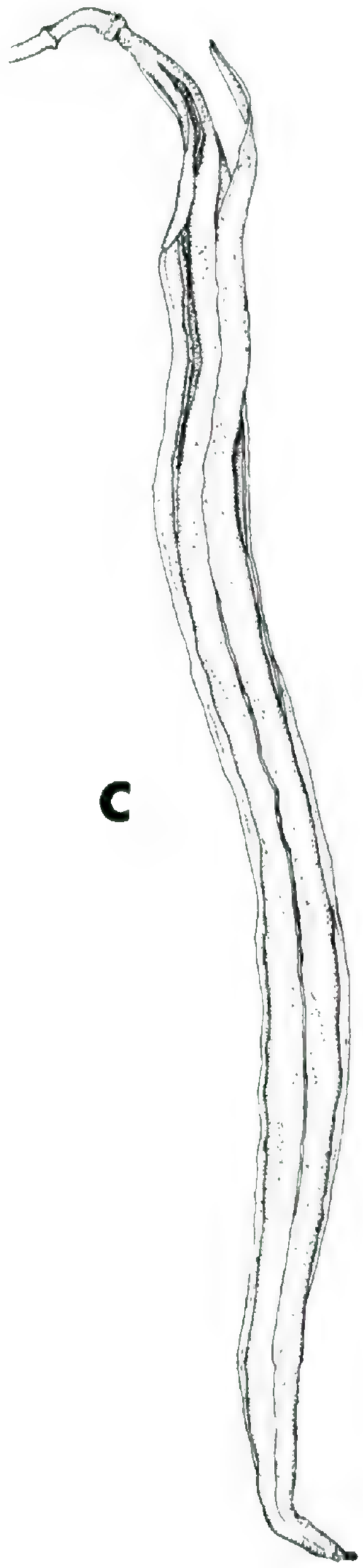
Additional collections examined: PERU. LORETO: Provincia de Requeña, Genaro Herrera, Río Ucuyali below Requeña, non-inundated upland forest on sandy soil, tree 30 m, flowers yellow, with red streaking in throat, leaves white beneath, bark smooth and powdery, 9 Dec. 1977, *Gentry et al. 21314* (MO).

BRAZIL. AMAZONAS: Manaus, Reserva Florestal Ducke, árvore 2205 do levantamento-fenológico 101, árvore de 25 m de altura por 30 cm de diâmetro, mata de terra firme, solo argiloso, 22 June 1966, *Rodrigues & Osmarino 8139* (INPA-17500), margem da estrada principal, lado direito, árvore de 30 m por 25 cm de diâmetro, de fuste ereto e copa de 5 m de diâmetro, desfolhada, ocasional na mata de terra firme, cálice verde ferrugíneos com lacíneas roxas nas bordas, corolla amarela com listra vermelhoéscuras e pelos brancos no tubo corolínico, "pau-darco amarelo," 20 Oct. 1970, *Rodrigues 8973* (INPA-28359). Estrada Manaus-Itacoatiara, Km 105, margem da estrada, ocasional na mata de terra firme, árvore de 25 m no inicio da floracão, fuste de 20 cm de diâmetro na base, flores amarelas, 11 Sep. 1965, *Rodrigues & Loreiro 7117* (INPA-15779, MO). Estrada Manaus-Itacoatiara, Km 104, árvore de 30 m de altura por 33 cm de diâmetro, fuste de 24 m de comprimento, circunferência do fuste na base 106 m, no meio 86 cm e no ápice 56 cm, copa de 6 m de altura por 8 de largura, "pao d'arco," 24 May 1968 (sterile), *Coelho, Lima & Osmarino s.n.* (INPA-21246). PARA: Belterra, árvore, madeira branca na periferia e preta no interior, casca lisa, 29 June 1947, *Black F1047-969* (IAN). Belterra, virgin upland forest, 570 ft, tree 123 ft tall, 39" diam., wood with odor of horse urine, 3 July 1947, *Yale Project 134, F-10* (US).

The most distinctive characteristic of this species is the canescent, appressed-stellate leaf tomentum beneath. This characteristic is shared only with *T. subtilis* Sprague & Sandw., which may be the closest relative of *T. incana*. *Tabebuia subtilis* differs chiefly in its much larger (10–17 mm by 9–12 mm), more finely tomentose calyx and elongate (3–10 mm long) inflorescence bracts. That species is a shrub or small tree of the Guayana uplands; *T. incana* is a large, 25–30 m tall canopy tree of Central Amazonia.

Manaosella cordifolia (DC.) A. Gentry, comb. nov.—FIG. 3.





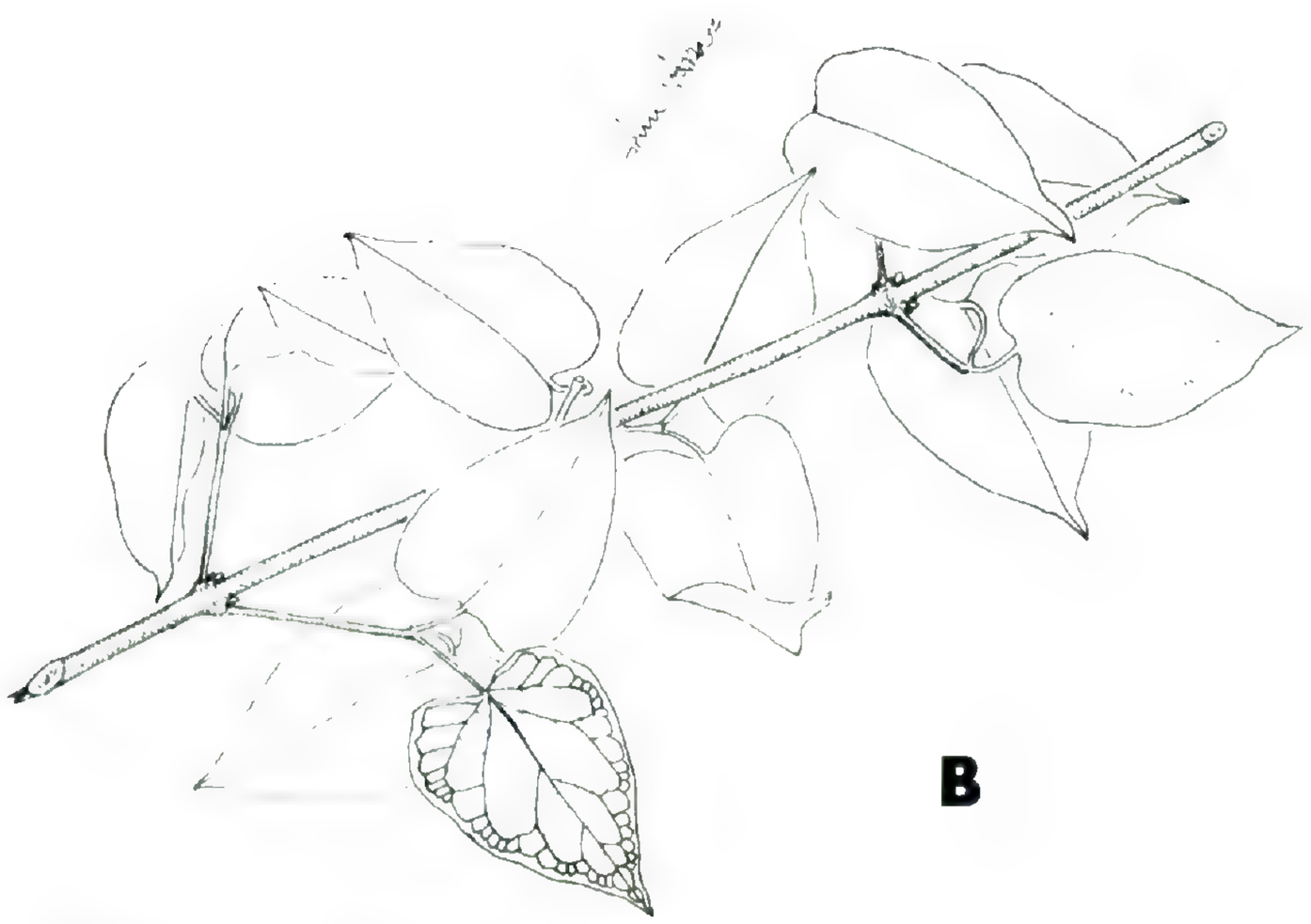


Figure 3. *Manaosella cordifolia* (DC.) A. Gentry.—A. Habit (×3/5). [After *Ducke s.n.*, RB-35644 (MO)].—B. Sterile branch (×3/5). [After *Ducke s.n.*, RB-35644 (MO)].—C. Fruit (×3/5). [After *Gentry 13319* (MO)].

Bignonia cordifolia DC., Prodr. 9: 162. 1845. TYPE: Brazil, Bahia, *Martius s.n.* (M).
Alsocydia cordata Mart. ex DC., Prodr. 9: 163. 1845, nom. nud., pro syn.
Bignonia platydactyla Barb. Rodr., Vellosia, ed. 2, 1: 51. 1891. TYPE: Brazil, Amazonas, *Barbosa Rodriques s.n.* (not seen).

Manaosella platydactyla (Barb. Rodr.) J. C. Gom., Arch. Jard. Bot. Rio de Janeiro 9: 85. 1949.

The generic affinities of *Bignonia cordifolia*, known only from Martius's type collection from Bahia, Brazil, have been a mystery for well over a century. In 1891 Barboso Rodrigues described from Manaus in Amazonian Brazil another species of Bigoniaceae with similar large inflated calyces and heart-shaped cordate leaves. Neither he nor any subsequent author ever noted the relationship of this Amazonian plant with *B. cordifolia*. *Bignonia platydactyla* is now assigned to the monotypic genus *Manaosella* and until recently has been supposed to be endemic to the region of Manaus. I have recently seen several collections of *Manaosella* which greatly extend both its distributional and morphological ranges. The new collections include: PARA: Belterra, *Black 46-1136* (IAN). Faz. Santa Olympia, Mun. Faro, *Black & Ledoux 50-10596* (IAN). Rio Tapajos, *Ducke s.n.* (RB-18415) (RB, MO). RONDONIA: Pôrto Velho, *Black s.n.* (IAN). MINAS GERAES: Manhumirim, *Hatschbach & Ahumada 31389* (MO). 31 km E of Poté, *Davidse et al. 11497* (MO).

Reexamination of the type photograph of *Bignonia cordifolia* from the perspective of these additional collections proves it quite indistinguishable from *Manaosella*. The older basionym of *B. cordifolia* must be retained in *Manaosella* and necessitates the new combination proposed here.

COMMENTARY ON THE MISTLETOES OF PANAMA[1]

JOB KUIJT[2]

ABSTRACT

An updated listing is provided for Panamanian genera and species of Loranthaceae (*Cladocolea*, *Gaiadendron*, *Oryctanthus*, *Phthirusa*, *Psittacanthus*, *Struthanthus*, and possibly *Ixocactus*), Viscaceae (*Dendrophthora*, *Phoradendron*), and Eremolepidaceae (*Antidaphne*). Aside from certain nomenclatural changes, new records from Panama are: *Cladocolea oligantha* (Standley & Steyermark) Kuijt, possibly *Ixocactus hutchisonii* Kuijt, *Phoradendron annulatum* Oliver, *P. crassifolium* (Pohl) Eichler, *P. dichotomum* (Bertero) Krug & Urban, *P. dipterum* Eichler, *P. quadrangulare* (H.B.K.) Krug & Urban, *P. robustissimum* Eichler, *Psittacanthus nodosus* (Desr.) G. Don, *Struthanthus quercicola* (Cham. & Schlecht.) Blume, and S. aff. *dichotrianthus* Eichler. In addition, the following new species are described: *Dendrophthora panamensis* Kuijt, *Psittacanthus hamulifer* Kuijt, and *P. pusillus* Kuijt. Six further species are recognized but remain unnamed because of difficulties inherent in *Phoradendron*, raising the total number of Panamanian mistletoes to at least 45 species.

In the years since Rizzini's (1960) treatment of the mistletoes of Panama appeared, various new points of view have arisen with regard to some of his interpretations, and numerous new relevant facts have emerged. The following is offered as a series of emendations.

Perhaps the most important broader change which has occurred in the intervening years is the acceptance of two or even three separate mistletoe families (Barlow, 1964; Kuijt, 1968). All three of these families are represented in Panama, Eremolepidaceae (*Antidaphne*), Viscaceae (*Dendrophthora*, *Phoradendron*), and Loranthaceae, s.s. (*Cladocolea*, *Gaiadendron*, *Oryctanthus*, *Phthirusa*, *Psittacanthus*, *Struthanthus* (incl. "*Phrygilanthus*" *panamensis*) and possibly *Ixocactus*. My present comments, however, are organized in an alphabetical fashion. In all cases, this commentary applies to a Panamanian context, its usefulness to adjacent geographic areas being untested. For species merely listed below, the reader is referred to the critical literature cited under each genus.

KEY TO THE GENERA OF PANAMANIAN MISTLETOES

a. Phyllotaxy alternate throughout.
  b. Flowers with conspicuous, aborted organs of the opposite sex; spikes lacking distal leafy organs; petals conspicuous, 4; style at least 4 mm long ..... 2. *Cladocolea*
  bb. Flowers lacking aborted organs; pistillate spikes normally with small, distal leaves which may expand into full size after flowering; petals 2(3), lacking in staminate flowers, less than 0.5 mm in the pistillate flowers; style less than 1 mm long ..... 1. *Antidaphne*

aa. Phyllotaxy decussate or whorled.
  c. Flowers single (not in diads, triads, or longitudinal series), individually in axillary positions on the main stem, on spikes, or on racemes.

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[1] Acknowledgements are due to the National Research Council of Canada for financial support; to Dr. Karel U. Kramer for the Latin diagnoses; and to curators of several herbaria for assistance rendered.

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0026-6493/78/0736–0763/$02.95/0

d. Inflorescence lacking, the flowers 1–several per leaf axil; plants squamate, the young stems obviously compressed ... 5. *Ixocactus* (included tentatively only)
dd. Inflorescence a raceme or spike; plants leafy, the stems terete or slightly compressed.
e. Inflorescence a spike, the flowers or fruits sessile, often in depressions, always flanked by 2 minute, separate bracteoles; flowers less than 5 mm long ... 6. *Oryctanthus*
ee. Inflorescence a raceme, the individual flowers pedicellate, the pedicel supporting a bract and 2 fused bracteoles; flowers more than 8 mm long ... 10-5. *Struthanthus panamensis* (Rizz.) Barlow & Wiens
cc. Flowers sessile above bracts, usually in longitudinal series, or in diads or triads.
f. Flowers sessile in depressions above the inflorescence bracts, always lacking individual bracteoles, and never in diads or triads; plants squamate or leafy.
g. Anthers unilocular; plants squamate or leafy; flowers in single or multiple series above the bracts ... 3. *Dendrophthora*
gg. Anthers bilocular; plants leafy; flowers always in multiple series above the bracts ... 7. *Phoradendron*
ff. Flowers and/or triads (diads) stalked, not in depressions, the flowers always with individual bracts or bracteoles; plants leafy.
h. Plants dioecious, the flowers with aborted stamens or style.
i. Filaments thin; inflorescence a simple raceme ... 10. *Struthanthus*
ii. Filaments stout, the upper ones with lateral depressions; inflorescence a panicle ... 8-1. *Phthirusa adunca* (Meyer) Maguire
hh. Plants with the flowers hermaphroditic.
j. Flowers golden yellow, subtended by green leafy bracts; parasites or seemingly epiphytes on tree branches, or terrestrial ... 4. *Gaiadendron*
jj. Flowers at least partly red or orange, not subtended by leafy bracts; parasites on tree branches.
k. Flowers less than 4 mm long; epicortical roots from base of plant; fruit with endosperm ... 8-2. *Phthirusa pyrifolia* (H.B.K.) Eichler
kk. Flowers more than 10 mm long; epicortical roots lacking; fruit without endosperm ... 9. *Psittacanthus*

1. ANTIDAPHNE Poepp. & Endl., Nov. Gen. & Sp. Pl. 2: 70, *tab. 199*. 1838.

The genus and two others not occurring in Central America (*Eremolepis* and *Eubrachion*) have been placed in a separate family, Eremolepidaceae. The species below, the only one in Central America, ranges from Mexico and Guatemala into South America.

Critical literature: Rizzini, 1956; Kuijt, 1964, 1968.

1. **Antidaphne viscoidea** Poepp. & Endl., Nov. Gen. & Sp. Pl. 2: 70, *tab. 199*. 1838.

This is the only species of the genus in Panama. The following are recent collections.

CHIRIQUÍ: Slopes on Cerro Horqueta, 1650 m, *Croat 26950* (MO). Lava fields near Volcán, 4600 ft, *Duke 9178* (MO). 1 mi from El Volcán, *Ebinger 774* (MO). 3 km NW of Boquete, 1320 m, *Nee 10627* (MO). Roadsides S of Boquete, 1050–1100 m, *Nee 10647* (MO). 1 km NE of El Hato del Volcán, 1440 m, *Nee 14128* (MO). S side of El Hato del Volcán, 1390 m, *Nee 14147* (MO). DARIÉN: Summit of Pico Tacarcuna, 1850 m, *Gentry et al. 16904* (MO). PANAMÁ: Road from El Llano to Cartí-Tupile, 12 km above Pan-Am. Highway, 200–250 m, *Croat 22906* (MO).

2. CLADOCOLEA Van Tieghem, Bull. Soc. Bot. France 42: 166. 1895.

Erect or scandent *parasitic shrubs*, glabrous or short-pubescent; lateral branches (including inflorescences) often emerging in a pseudo-endogenous fashion; epicortical roots on stems or at the base of the plant or absent. *Leaves* decussate, alternate, or irregularly arranged, simple, with pinnate venation, sometimes reduced to scales. Plants *dioecious* or with *flowers hermaphroditic*; in the former case aborted organs of the opposite sex usually present. *Inflorescence* normally a determinate spike, capitulum, dichasium, or raceme, in some species having undergone loss of the terminal flower or having been reduced to a single flower with 1 pair of bracts; lateral flowers ebracteolate, single in the axils of squamate (sometimes caducous) or foliaceous bracts. *Flowers* pale green to pale yellow, sessile or pedicellate, 4-, 5-, or 6-partite; stamens fused with the perianth members, dimorphic or monomorphic, with 4 thecae; pollen rounded triangular, sometimes with a triradiate groove and included triangular prominence, otherwise smooth; style often contorted or geniculate, especially in the upper portion. *Fruit* a 1-seeded berry with endosperm; embryo dicotyledonous, elongate, or globular, the haustorial disc weakly developed.

This generic name has lain dormant since 1895 and has recently been revived to accommodate various species assigned to *Struthanthus*, *Phthirusa*, and *Oryctanthus*, plus a number of previously undescribed species, making a total of 23 species. Most of these species are found in Mexico but a few are South American. *Cladocolea oligantha*, however, is Guatemalan except for the remarkable disjunct population represented by the two collections below. Most members of the genus are characterized by a determinate spike of sessile, ebracteolate flowers. In the case of the Panamanian species the spike is reduced to three flowers, but the spikes occur in two slightly different forms, depending upon the age of the branch supporting them. The type of *C. oligantha* is from Guatemala.

Critical literature: Kuijt, 1975.

1. **Cladocolea oligantha** (Standley & Steyermark) Kuijt, J. Arnold Arbor. 56: 317. 1975.

Struthanthus oliganthus Standley & Steyermark, Publ. Field Mus. Nat. Hist., Bot. Ser. 23: 154. 1944.

Plants *dioecious*, sparsely branched, completely glabrous, with sympodial growth; stems rather stout and straight, terete, first light colored, later dark brown and often with a sprinkling of rather large, transverse lenticels; 1-year-old wood (bearing secondary inflorescences) with shrunken bark, as if cortex very fleshy; no basal or stem roots seen. *Leaves* alternate, 20–30(–45) mm long, 8–10 (–16) mm wide, lanceolate to oblanceolate, acute to rounded at the apex, long-tapering at the base into a petiole 2–4 mm long and 0.5–2 mm thick; midvein running into the apex, other veins often obscure, pinnate except for 2 large, basal lateral veins running halfway down the length of the blade. *Inflorescences* of 2 types: (1) primary, on current year's growth, mostly single (rarely with a superposed inflorescence), axillary, simple dichasia on peduncles 4–5(–10) mm long and 1 mm thick, the bracts of 2 lateral flowers caducous, the 3 flowers

in one plane; and (2) secondary, developing on year-old growth, bearing 1 or 2 small but normal foliage leaves at the very base, deceptively like primary leaves, the flowers 4–6, one of which is terminal, the others crowded nearby, spirally arranged. *Flowers* said to be reddish, ca. 5 mm long and 2 mm wide when in (clavate) bud, tetramerous; anthers 1.5 mm long, inserted in the middle of the petals, with projecting connective and 4 pollen sacs; stamens and petals monomorphic; style straight or nearly so, at least 4 mm long, the stigma inconspicuous. *Fruit* red, becoming black, 7 mm long, 5 mm wide, ovoid, smooth; embryo dicotyledonous, nearly 4 mm long, clavate.

PANAMÁ: Vicinity of Las Lajas bridge, Panama National Highway, *Bartlett & Lasser 16645* (MO). Near beach at Nueva Gorgina, on *Bursera tomentosa*, *Duke 4504* (GH, MO, US).

3. DENDROPHTHORA Eichler, Fl. Bras. 5(2): 102. 1868.

The genus is distinguished from *Phoradendron* by its unilocular anthers (*Phoradendron* has bilocular ones). This distinction is inconvenient but apparently consistent. It should be mentioned that the statement "cataphylls poorly developed" in the earlier Panamanian treatment is unreliable by way of a generic feature, as many *Dendrophthora* species have cataphylls (for example, all Panamanian species but *D. squamigera*). A fifth species, *D. ambigua* Kuijt (Kuijt, 1961b) may be expected in Panama, as it occurs both in Costa Rica and in Colombia-Ecuador. As in the case of others, it may easily be confused with *Phoradendron* spp.; however, it has a uniquely variable inflorescence type (Kuijt, 1961b, 1964).

Critical literature: Kuijt, 1961b, 1963b, 1964.

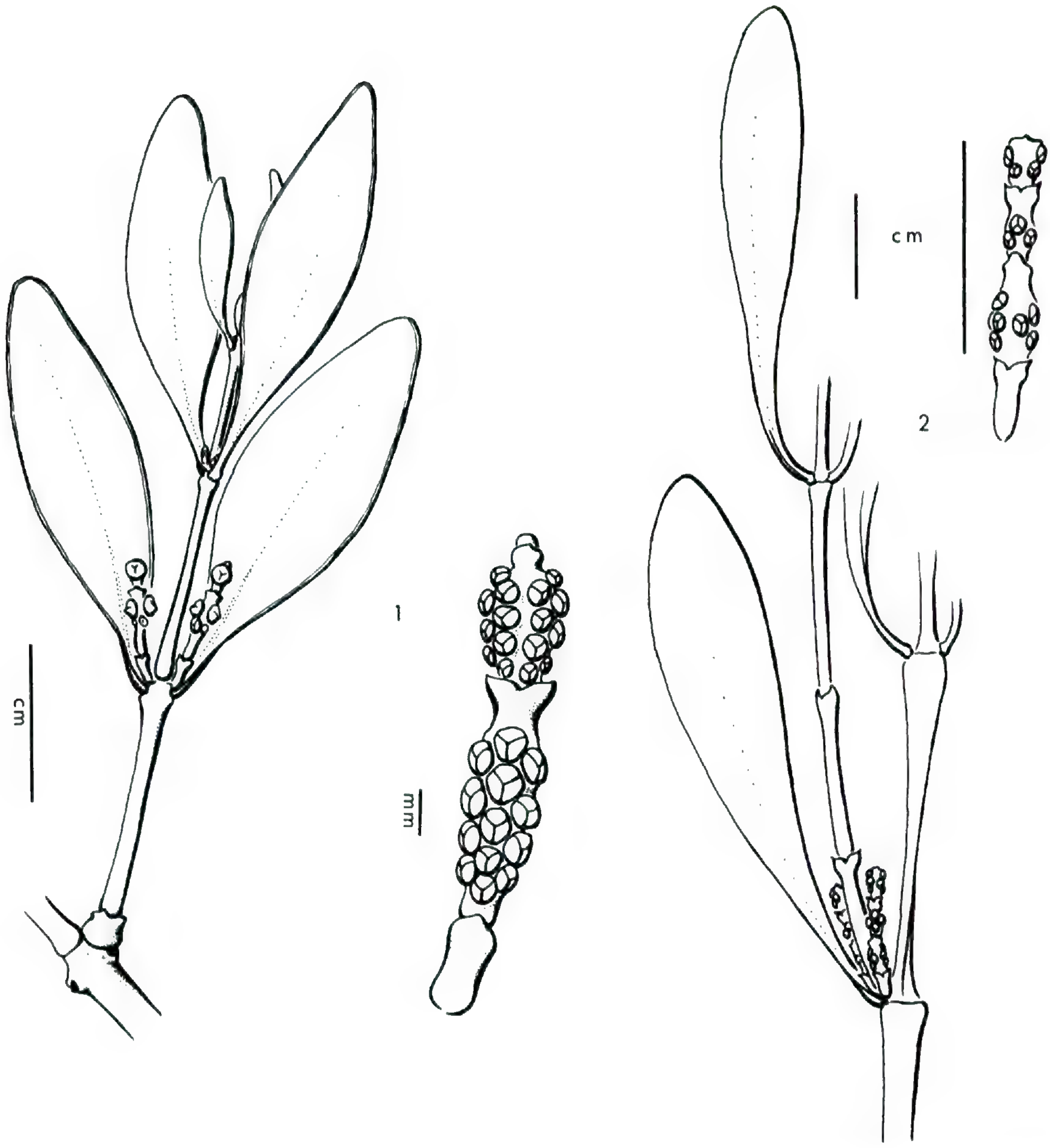
a. Plants leafy; flowers in 3 series above each fertile bract (except sometimes the small, terminal internodes); inflorescence with 2–3 fertile internodes.
  b. Plants monoecious; leaves broadly obovate; flowers more than 6 per bract ..... 1. *D. costaricensis* Urban
  bb. Plants dioecious; leaves lanceolate to rhombic or spatulate; flowers fewer than 6 per bract in *female plants only*.
    c. Lateral branches usually with 2 pairs of widely spaced basal cataphylls at least 7 mm from each other or above the axil; young stems compressed, with ridges ..... 4. *D.* sp.
    cc. Lateral branches with 1 (rarely 2) pairs of basal cataphylls less than 5 mm from each other or above the axil; young stems more or less terete, lacking ridges ..... 2. *D. panamensis* Kuijt
aa. Plants squamate, olive green to brown; flowers in a single series above each fertile bract; inflorescence usually with a single fertile internode ..... 3. *D. squamigera* (Benth.) Kuntze

1. **Dendrophthora costaricensis** Urban, Ber. Deutsch. Bot. Ges. 14: 285. 1896.

Phoradendron allenii Trelease, Ann. Missouri Bot. Gard. 27: 307. 1940.
P. crispum Trelease, Gen. Phor. 17. 1916.

2. **Dendrophthora panamensis** Kuijt, sp. nov.—FIG. 1.

Frutex glaber, ramosissimus, dioecus; internodia novella superne pauce applanata, inferne quadrangularia; rami laterales cataphyllis basalibus uni-(raro bi-)jugis, 2 ad 3 mm supra axillam



Figures 1–2.—1. *Dendrophthora panamensis* Kuijt, the (pistillate) type at left (*Liesner 1305*), a staminate spike at right (*Mori, Kallunki & Gentry 4703*).—2. *Dendrophthora* sp. No. 4 (*Croat 26949*).

positis. Folia rhomboidea ad lanceolata, usque ad 4 × 1.5 cm. Spica pistillata 1–1.5 cm longa, internodio sterili singulo, fertilibus tribus, floribus ternis pro bractea. Fructus baccatus, paulum compressus, circ. 2 mm diam. Spica staminata similis sed floribus pro bractea fertili usque ad 14.

Glabrous, much branched (percurrent) and brownish green *mistletoes*, the young internodes somewhat flattened above and slightly quadrangular below, soon becoming terete; lateral branches with one pair of inconspicuous, very basal cataphylls, sometimes followed by a second several mm higher. *Leaves* thin, to 4 cm long and 1.5 cm wide, thin, rhombic to lanceolate, with clearly defined

callused margin, the apex acute to rounded, the base cuneately tapered into a petiole about 3 mm long. *Dioecious*. *Pistillate spike* 1–1.5 cm long, slender, with 1 sterile internode and 3 fertile ones, the latter with ca. 3 flowers per bract (1 flower per bract on the terminal internode) on the distal portion of the internode. *Fruit* a compressed berry 2 mm in diameter. *Staminate spike* of similar size and composition, but with up to 14 orange yellow flowers per fertile bract in 1b arrangement (cf. Kuijt, 1963b), and sometimes a second sterile internode; anther bean shaped, unilocular, less than 0.5 mm long.

This is an inconspicuous species easily mistaken for a *Phoradendron*, but with clearly unilocular (though extremely small) anthers. *Dendrophthora panamensis* is a member of the *D. costaricensis* group of subgenus *Paradendrophthora*, as also indicated by the flattened berries which occur only in that subgenus (Kuijt, 1961b, 1964).

TYPE: PANAMA. SAN BLAS: Primary forest along newly cut road from El Llano to Cartí-Tupile, continental divide to 1 mi from divide, 300–500 m, *Liesner 1305* (MO, holotype; LEA, isotype).

Other material examined: PANAMÁ: El Llano-Cartí Road, 12.7 km from Inter-American Highway, wet forest, 350 m, *Mori, Kallunki & Gentry 4703* (MO, LEA).

3. **Dendrophthora squamigera** (Benth.) Kuntze, Rev. Gen. 2: 505. 1891.

D. biserrula Eichler, Fl. Bras. 5(2): 104. 1868.

4. **Dendrophthora** sp.—FIG. 2.

Much branched, stiffly erect *shrub* with internodes to 4 cm long, compressed, with 2 sharp ridges, becoming terete in age; percurrent branches without cataphylls; lateral branches with 2 (rarely 1) pairs of cataphylls widely spaced, the lowest 7–20 mm above axil, the second pair somewhat more above the first pair. *Leaves* narrowly spatulate, to 6 cm long and 1.5 cm wide, with long-tapering bases and obtuse apices. *Spikes* 1 per axil, or 2 flanking each lateral branch, to 2.5 cm long with 3–4 fertile internodes, basal cataphylls lacking (rarely with 1 pair), 3–4 flowers per bract in 3 series in the middle of fertile internodes, the terminal internode very blunt.

The absence of anthers deprives us of proof that this indeed is a *Dendrophthora* rather than a *Phoradendron*; the plant is pistillate with nearly mature spikes. However, its general appearance, especially the widely spaced, usually double set of basal cataphylls, suggests a *Dendrophthora*. Even if it is, it may easily already have received a name under *Phoradendron*, and it seems better simply to draw attention to it.

CHIRIQUÍ: In and along wooded slopes on Cerro Horqueta, 1650 m, *Croat 26949* (MO).

4. GAIADENDRON G. Don, Gen. Syst. 3: 431. 1834.

1. **Gaiadendron punctatum** (Ruiz & Pavón) G. Don., Gen. Syst. 3: 431. 1834.

G. poasense Donnell Smith, Bot. Gaz. (Crawfordsville) 56: 61. 1913.

Rizzini's suggestion that *Gaiadendron* must probably be returned to *Phrygilanthus* sensu Eichler has not been supported by subsequent work. Barlow & Weins (1973) have shown *Phrygilanthus* to be a very heterogenous group which cannot be retained as such. *Gaiadendron* according to Barlow & Wiens is best treated as a monotypic genus with a single polymorphic species, *G. punctatum*. Whether or not this is a defensible view, all Central American material is clearly referable to *G. punctatum*. It is of some interest that in this area the species occurs both at the diploid and tetraploid levels (Barlow & Wiens, 1971). The genus has hermaphroditic flowers, my previous description of *G. punctatum* as a monoecious species (Kuijt, 1964) being in error.

Critical literature: Barlow & Wiens, 1971, 1973; Kuijt, 1963a, 1964.

5. Ixocactus Rizz., Arch. Jard. Bot. Rio de Janeiro 12: 118. 1952.

1. **Ixocactus hutchisonii** Kuijt, Brittonia 19: 62. 1967.

A small, olive green, squamate *shrub* with decussating, minute scale leaves, the internodes to 7 cm long, much compressed, oblong to somewhat rhombic; lateral branches (or flowers) at most 5 per axil. *Flowers* perfect, 2 mm long and 1 mm thick in bud; petals 4 (3), broadly oval, each with a sessile anther provided with 2 minute pollen sacs dehiscing longitudinally, the pollen sacs with no more than 30 grains each, the anthers (sometimes pollen sacs of a single anther) often at different heights, at least in tetramerous flowers, the pollen commonly quadricolpate with a dense covering of stout spines and four conspicuous, longitudinal colps; style bluntly conical, persistent, the stigma capitate. *Fruit* an oval berry, at least 3.5 mm long and 2 mm thick.

This striking monotypic genus has so far been known only from two collections from Venezuela and Colombia. In the Stockholm Herbarium, however, there exists an early collection of *I. hutchisonii* apparently from Panama. The accompanying data are, unfortunately, very scanty: N. J. Andersson, Panama, April 1852. There are two separate sheets. Dr. Benkt Sparre, Curator of the Regnellian Herbarium, confirms that Andersson was indeed in Panama in April, 1852, but that Andersson was a rather careless collector. The possibility that material from the previous collecting area (Isla Puna outside Guayaquil in Ecuador) was invadvertently labelled "Panama" can be neither excluded nor confirmed. It is also known that Andersson visited the Pearl Islands (Panama) at about this time, but his diary provides no further information on the matter. I feel there is no alternative but to add *Ixocactus* to the *Flora of Panama*, even though on a tentative basis only. The brief description is taken from Kuijt (1967) where illustrations may also be found.

6. Oryctanthus Eichler, Fl. Bras. 5: 87. 1868.

This genus has recently been monographed, resulting in a number of nomenclatural and taxonomic changes from both Rizzini's (1960) treatment of Panama and mine (Kuijt, 1964) for Costa Rica, as indicated below.

Critical literature: Kuijt, 1961a, 1976a.

a. Flowers and fruits perpendicular to the inflorescence axis.
  b. Stems terete even when young ---------- 3. *O. occidentalis* (L.) Eichler
  bb. Stems strongly compressed or angular when young ---------- 2. *O. cordifolius* (Presl) Urban

aa. Flowers and fruits inclined forward.
  c. Plants small; leaves petiolate, rather thin, the midrib running into the leaf apex; stems angular and with furfuraceous lines when young; spikes slender, always with a distinct peduncle, never in terminal compound groups ---------- 4. *O. spicatus* (Jacq.) Eichler[3]
  cc. Plants coarse; leaves short-petiolate or clasping, leathery, the midrib (if visible) not running into the apex; stems terete, with a general (not lined) furfuraceous covering when young; spikes stout, with a thick peduncle or nearly sessile, axillary, in some also in terminal compound groups ---------- 1. *O. alveolatus* (H.B.K.) Kuijt

1. **Oryctanthus alveolatus**[4] (H.B.K.) Kuijt, Bot. Jahrb. Syst. 95: 504. 1976.

Loranthus alveolatus H.B.K., Nov. Gen. Sp. Pl., Quarto text, 3: 444. 1820.
Oryctanthus amplexicaulis (H.B.K.) Eichler, Fl. Bras. 5(2): 88. 1868.
O. botryostachys Eichler, Fl. Bras. 5(2): 89. 1868.

This is a widespread and taxonomically difficult complex which in past works has been referred to as *O. amplexicaulis* and *O. botryostachys* in Central America and parts of South America. It may well be that two such variants (one amplexicaul and with terminal compound inflorescences, the other petioled and with only axillary spikes) warrant some subspecific status in the area, but at present such a delimitation is impossible in South America. It should be noted that Rizzini (1960) used the name *O. spicatus* with reference to the second variant, known elsewhere as *O. botryostachys*.

2. **Oryctanthus cordifolius** (Presl) Urban, Bot. Jahrb. Syst. 24: 30. 1898.

This is an easily recognized species by its combination of large, clasping leaves and sharp-angled stems.

3. **Oryctanthus occidentalis** (L.) Eichler, Fl. Bras. 5(2): 89. 1868.

Frequently confused with some plants of *O. alveolatus*, and more rarely *O. cordifolius*, *O. occidentalis* nevertheless does not intergrade with these species, and can always be identified when using the keys consistently. The species has a parallel geographic range and taxonomic complexity as compared to *O. alveolatus*, but also occurs on Jamaica.

4. **Oryctanthus spicatus** (Jacq.) Eichler, Fl. Bras. 5(2): 89. 1868.

Notwithstanding inclusion of this name in Rizzini's (1960) treatment (see above under *O. alveolatus*), authentic *O. spicatus* material does not seem to have been collected yet from Panama. This is surprising since its total geographic range stretches from Guatemala to Peru, the species being especially

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[3] See note under *O. spicatus*.
[4] For further synonymy, see Kuijt (1976a).

common in both Costa Rica and Colombia. As it seems reasonable to expect this inconspicuous mistletoe at least in the mountainous northerly portions of Panama, it is here tentatively included.

7. PHORADENDRON Nuttall, J. Acad. Nat. Sci. Philadelphia, ser. 2, 1: 185. 1847.

I am disappointed to find that I can no more construct a key to Panamanian *Phoradendron* than I can identify several unnamed species—and for very similar reasons. The distinctions between *P. quadrangulare* and the almost exclusively Caribbean *P. trinervium*, for example, need first to be clarified, and I am presently not in a position to do this.

Critical literature: Kuijt, 1959; Trelease, 1916, 1940.

1. **Phoradendron acinacifolium** Eichler, Fl. Bras. 5(2): 117. 1868.

Phoradendron robaloense Woods. ex Rizz., Ann. Missouri Bot. Gard. 47: 282. 1960.

Although the two collections below correspond to Costa Rican plants (Kuijt, 1964), the specific epithet here used belongs to Brazilian material, and is possibly inappropriate.

CHIRIQUÍ: Bajo Mona, Robalo Trail, 1500–2100 m, *Allen 4838* (MO, holotype of *P. robaloense*). COLÓN: East ridge, *Duke 15274* (MO).

2. **Phoradendron angustifolium** (H.B.K.) Nuttall, J. Acad. Nat. Sci. Philadelphia, ser. 2, 1: 185. 1847.

Viscum stenophyllum Spreng., Syst. Veg. 1: 487. 1825, non *Phoradendron stenophyllum* Trelease, Gen. Phor. 81. 1916.
Loranthus angustifolius H.B.K., Nov. Gen. Sp. Pl. 3: 442. 1820.
Viscum angustifolium (H.B.K.) DC., Prodr. 4: 281. 1830.
V. ensifolium Pohl in DC., Prodr. 4: 281. 1830.
Phoradendron ensifolium (Pohl) Nuttall, J. Acad. Nat. Sci. Philadelphia, ser. 2, 1: 185. 1847.
P. corynarthron Eichler, Fl. Bras. 5: 115. 1868.
P. cooperi Trelease, Gen. Phor. 67. 1916.
?*P pringlei* Trelease, Gen. Phor. 60. 1916.
P. tonduzii Trelease, Gen. Phor. 67. 1916.
P. dodgei Trelease, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 405. 1937.
P davidsoniae Standley, Publ. Field Mus. Nat. Hist., Bot Ser. 22: 17. 1940.
P. novae-helveticae Trelease, Ann. Missouri Bot. Gard. 27: 307. 1940.

As visualized here, we are concerned with a not exceptionally polymorphic species ranging from Costa Rica into Peru, Bolivia, and Brazil. The variability in leaf width and length, but also in flower seriation, has brought about the excessive synonymy above.

3. **Phoradendron annulatum** Oliver, Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1864: 176. 1865.

See comments under No. 19.

CHIRIQUÍ: Boquete District, Volcán de Chiriquí, 10,000 ft. *Davidson 996* (F).

4. **Phoradendron crassifolium** (Pohl) Eichler, Fl. Bras. 5(2): 125. 1868.

The species is unmistakable because of the production of spikes in the axils of intercalary cataphylls (Kuijt, 1959), a feature not found in any other Central American mistletoe. Superficially, the species resembles *P. woodsonii* and species No. 18 where intercalary cataphylls are always sterile.

CANAL ZONE: 5 mi N of Gamboa, *Lazor & Blum 5333* (DUKE, MO). CHIRIQUÍ: Volcán, *Croat 10425* (DUKE, MO). Cerro Hornitos, 40 km NW of Gualaca, 2238 m, *Mori & Bolten 7512* (MO). COLÓN: Santa Rita Ridge, *Foster 1720* (DUKE). DARIÉN: El Real, *Burch et al. 1060* (DUKE, MO). Forest near Pidiaque Peak, 800–1000 ft, *Duke 8070* (MO). PANAMÁ: Camino a Chepo, *Correa et al. 996* (DUKE, MO). Cerro Jefe, 2100–2200 ft, *Duke 15222* (MO). Cerro Azul, *Dwyer 1382, 2068* (both MO). Cerro Jefe, 800–1000 m, *Gentry 2888* (MO). Punta de Cerro Jefe, *Gómez-Pompa et al. 3081* (MO). 16–20 km above Pan-Am. Highway on road from El Llano to Cartí-Tupile, 400 m, *Kennedy 2702* (MO). Road past Cerro Azul 20 km from junction with road through Tocumen, *Mori & Kallunki 2210* (MO). VERAGUAS: Isla de Coiba, *Dwyer 2337* (MO).

5. **Phoradendron dichotomum** (Bertero) Krug & Urban, Bot. Jahrb. Syst. 24: 48. 1897.

Assignment of the two specimens cited below to *P. dichotomum* is tentative. They are both unusually stout as compared with Costa Rican material, the leaf pairs of the second collection 20 cm apart, and the leaves rather leathery. The same specimen is clearly staminate, while Costa Rican material was thought to be monoecious (Kuijt, 1964). In all other respects, especially the terminal spikes which as a regular feature are not known from other Central American species, the plants correspond to *P. dichotomum*. See the discussion in Kuijt (1964) of the geographical range of this mistletoe.

PANAMÁ: El Llano-Cartí road, 12.7 km from Inter-American Highway, on melastome, 350 m, *Mori et al. 4678* (MO). VERAGUAS: 5 mi W of Santa Fé, 800–1200 m, *Croat 23055* (MO).

6. **Phoradendron dipterum** Eichler, Fl. Bras. 5(2): 109. 1868.

This is an interesting species, here reported from Panama for the first time, thus linking South American collections with those from Costa Rica and further north (Kuijt, 1964). Panamanian material is similar to that from Costa Rica in having stems quadrangular rather than winged, but it differs somewhat in that the leaves are not clasping, and the spikes are rather small.

LOS SANTOS: Pocri, *Dwyer 2518* (MO).

7. **Phoradendron flavens** (Swartz) Griseb., Fl. Brit. W. I. 33. 1864.

P. quinquenervium Krause, Notizbl. Königl. Bot. Gart. Berlin 5: 264. 1912.
P. supravenulosum Trelease, Gen. Phor. 154. 1916.

See the discussion under *P. flavens* in Kuijt (1964).

8. **Phoradendron mucronatum** (DC.) Krug & Urban, Bot. Jahrb. Syst. 24: 352. 1897.

9. **Phoradendron obliquum** (Presl) Eichler, Fl. Bras. 5(2): 134. 1868.

Having studied the type material at Prague (*Haenke s.n.*, from Peru), I no longer doubt that Central American plants are conspecific with it. In particular, the type appears to have flowers of both sexes on the same spike, rendering it monoecious as the plants in Costa Rica (Kuijt, 1964) and Panama.

CANAL ZONE: 12 mi N of Gamboa, on *Xanthoxylum belizensis* Lundell, *Tyson 6653* (MO). 4 km NW of Gamboa, 50 m, *Nee 7540* (MO). DARIÉN: Vicinity of El Real along road to airport, on *Xanthoxylum*, *Croat 15443* (MO). PANAMÁ: Vicinity of El Llano, on *Vitex*, *Duke 5796* (MO). Cerro Jefe, 2700–3000 ft, *Tyson et al. 3282* (MO).

10. **Phoradendron piperoides** (H.B.K.) Trelease, Gen. Phor. 145. 1916.

11. **Phoradendron quadrangulare** (H.B.K.) Krug & Urban, Bot. Jahrb. Syst. 24: 35. 1897.

P. ceibanum Trelease, Gen. Phor. 110. 1916.
P. rensonii Trelease, Gen. Phor. 105. 1916.
P. venezuelense Trelease, Gen. Phor. 111. 1916.
P. paquitanum Trelease, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 405. 1937.
P. corynarthron Eichler var. *seibertii* Trelease, Ann. Missouri Bot. Gard. 24: 187. 1937.
P. seibertii Rizz., Ann. Missouri Bot. Gard. 47: 285. 1960.

Consistent application of the concept of *P. quadrangulare* as employed by Standley & Steyermark (1946) in the *Flora of Guatemala* results in at least the above synonyms from Costa Rica and Panama. Undoubtedly, more synonyms will accrue when this difficult species can be surveyed as a whole, as indicated in the further synonyms in Standley & Steyermark (1946) and Rizzini (1960). Only a few representative collections from Panama are listed below; the species may be expected at lower elevations throughout Panama.

BOCAS DEL TORO: Hill above RR station at Milla 7.5, an *Cassia reticulata*, *Croat & Porter 16364* (MO). CANAL ZONE: Diablo Heights, 10 m, *Nee 11151* (MO). 1.5 km SE of Pedro Miguel, 15 m, *Nee 10192* (MO). Just inland from Playa Kobbe, *Wilbur & Teeri 12993* (DUKE). PANAMÁ: Cerro Jefe, 2900 ft, *Dwyer & Hayden 8080* (MO, LEA). VERAGUAS: Road between San Francisco and Santa Fé, *Stern et al. 1929* (MO).

12. **Phoradendron robustissimum** Eichler, Fl. Bras. 5(2): 122. 1868.

P. pergranulatum Trelease, Ann. Missouri Bot. Gard. 27: 308. 1940.

This species has previously been reported from Venezuela, from Costa Rica to southern Mexico (Kuijt, 1964), and (as *P. pergranulatum* Trelease, based on a single specimen) from Panama. The latter specimen is clearly dichotomous as Costa Rican plants, but the others here cited also (or only) show percurrent branching.

CHIRIQUÍ: 1½ km NW of Boquete on road to El Salto, 1280 m, *Nee 10655* (MO, LEA). COCLÉ: El Valle, 800–1000 m, *Allen 777* (ILL, type of *P. pergranulatum* Trelease). El Valle de Antón, 1000–2000 ft, *Lewis et al. 2571* (MO, LEA). LOS SANTOS: 7 mi S of Las Tablas, *D'Arcy & Croat 4204* (MO). PANAMÁ: 7 mi S of Campana, 3–30 m, *McDaniel 8335* (DUKE).

13. **Phoradendron trinervium** Griseb., Fl. Brit. W. I. 314. 1860.

14. **Phoradendron undulatum** Eichler, Fl. Bras. 5(2):122. 1868.

P. gracilispicum Trelease, Gen. Phor. 130. 1916.

Trelease (1916) mentions two further specimens from Chiriquí (*Pittier 2932, 3312*) which I have not seen.

CHIRIQUÍ: Lava fields 2.2 mi E of Hato del Volcán, ***Luteyn 810*** (DUKE, MO).

15. **Phoradendron woodsonii** Trelease, Ann. Missouri Bot. Gard. 27: 308. 1940.

A rather small species; stems terete, the percurrent internodes with 2–4 pairs of sterile intercalary cataphylls. *Leaves* to 5.5 cm long and 2.5 cm wide, ovate to lanceolate, the margin callused, the base tapering into a short stout petiole. *Spikes* clustered at leafy nodes, ca. 5 cm long, consisting of 5 or 6 fertile and 2 or 3 sterile, short internodes. *Flowers* in 3 series above each bract, ca. 9 per bract, and near the middle of the internode, the terminal internode reduced and sharply pointed. *Fruit* short-ovate, ca. 2 mm thick, the petals closed.

This species is closely related to the unnamed species No. 18, but differs as there specified. Other near relatives are *P. crassifolium* and *P. piperoides*. Previously it was known from the type collection only.

CHIRIQUÍ: Cerro Hornitos, 40 km NW of Gualaca, 2238 m, *Mori & Bolten 7512* (MO). 3 km N of El Volcán, 5000 ft, *Tyson 5727* (MO). COCLÉ: Between Las Margaritas and El Valle, *Woodson et al. 1302* (ILL, type). PANAMÁ: La Campana, Cerro Campana, *Duke 10743* (MO, OS); *Ebinger 343* (MO). Road from Cerro Azul to Cerro Jefe, 2300–2700 ft, *Tyson 4312* (MO).

16. **Phoradendron** sp.—FIG. 3.

Light green plants; stems straight, terete, forking through formation of terminal spikes; lateral stems with 3 or 4 pairs of basal cataphylls mostly crowded at the base. *Leaves* to 8 cm long and 3.5 cm wide, palmate venation apparent on both surfaces, obovate to spatulate, the apex obtuse to emarginate, the base cuneately tapering to a short, stout petiole about 3 mm long. *Dioecious*; only pistillate plants seen. *Pistillate spikes* terminal and axillary, with very short sterile internodes and 3–4 fertile ones, each spike up to 2 cm long. *Flowers* mostly one above each bract but sometimes 2–5 in 1b (cf. Kuijt, 1963b) arrangement, or with 2 flowers very nearly above each other; petals and berries orange, ovate, at least 2 mm wide and 4 mm long when dry with closed petals, the base sunken in a conspicuous floral cup.

This species does not seem to be included in Trelease's (1916) monograph but may have been published subsequently. It is distinctive in its terminal spikes and forking habit, and in the flower position which sometimes mimics the 2a type (cf. Kuijt, 1963b) which is restricted to *Dendrophthora*. In the present species the two flowers which follow the apical one above each bract apparently are often reduced to a single one, and this one very nearly occupies a median position (Fig. 3, lower left). Although technically it cannot be established that the species is correctly assigned to *Phoradendron* (the collections are pistillate, and the generic distinction from *Dendrophthora* relies mostly on anther struc-

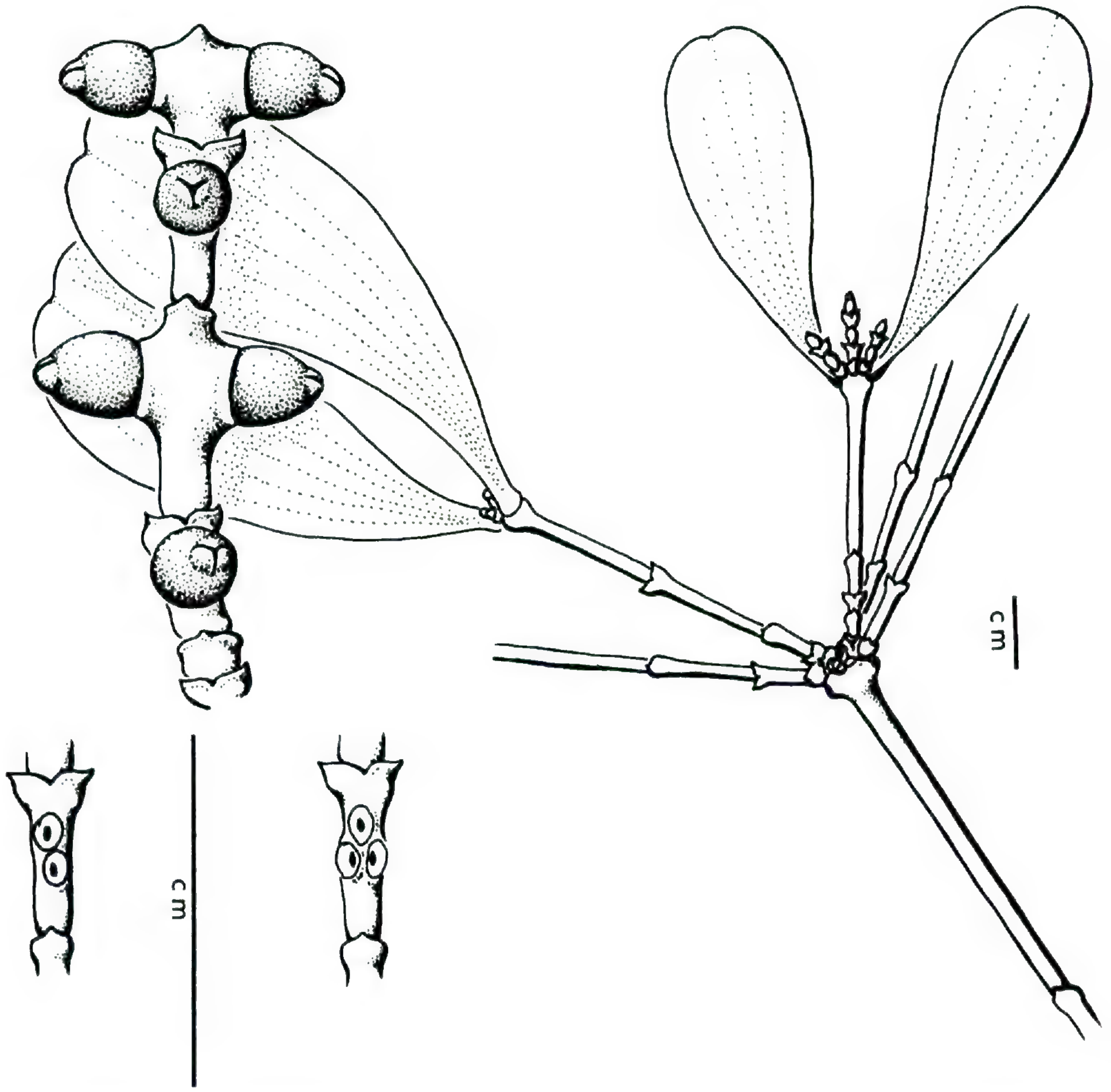


FIGURE 3.—*Phoradendron* sp. No. 16, habit (*Nee 10880*) and inflorescence details (*Nee 7420*).

ture), it is here placed in the former genus because of its forking habit and multiple cataphylls, neither of which feature is known from continental *Dendrophthora*.

CANAL ZONE: Summit Garden, 80 m, *Nee 7420* (MO, LEA). Along Chagres River, ½ km S of Fort San Lorenzo, sea level, *Nee 10880* (MO, LEA). DARIÉN: Puerto Saint Dorotea, on beach, *Dwyer 2260* (MO).

17. **Phoradendron** aff. **racemosum** (Aubl.) Krug & Urban, Bot. Jahrb. Syst. 24: 46. 1897.

Large plants, the internodes up to 7 cm long, distally compressed when young, soon becoming terete; cataphylls on lateral branches 1 pair, rarely 2 or 3, about 5 mm above base, none on percurrent internodes. *Leaves* to 15 cm

long and 6 cm wide, rather thin, ovate, the venation pinnate, the midvein very prominent below, the petiole ca. 15 mm long, gradually tapering into the base of the blade, the apex rounded. *Spikes* lax or even sinuous, lacking basal cataphylls, the peduncle 5–7 mm long, the internodes to 3 cm long, the bracts with ca. 15 flowers mostly in 2 series, the mature spike up to 9 cm long. *Berries* more or less spherical, 4–5 mm in diameter, the perianth inflexed.

The specimen cited below is undoubtedly related to *P. racemosum* but may not be conspecific with it.

True *P. racemosum* is known from the northerly Caribbean islands and from the French Guyana-Venezuela area (Trelease, 1916). Our Panamanian material differs in having compressed young stems, large berries (4–5 mm, about twice the size of those of true *P. racemosum*), spikes up to 9 cm long, and the fertile internodes longer and with more flowers, mostly in two series. All flowers on the plant seem to be pistillate, while Trelease implies a monoecious condition for *P. racemosum*.

CHIRIQUÍ: Cerro Colorado, along road between San Felix and Cerro Colorado, 2.3 km from turn-off to Escopeta, 1000 m, *Croat 37069* (MO).

18. **Phoradendron** sp.—FIG. 4.

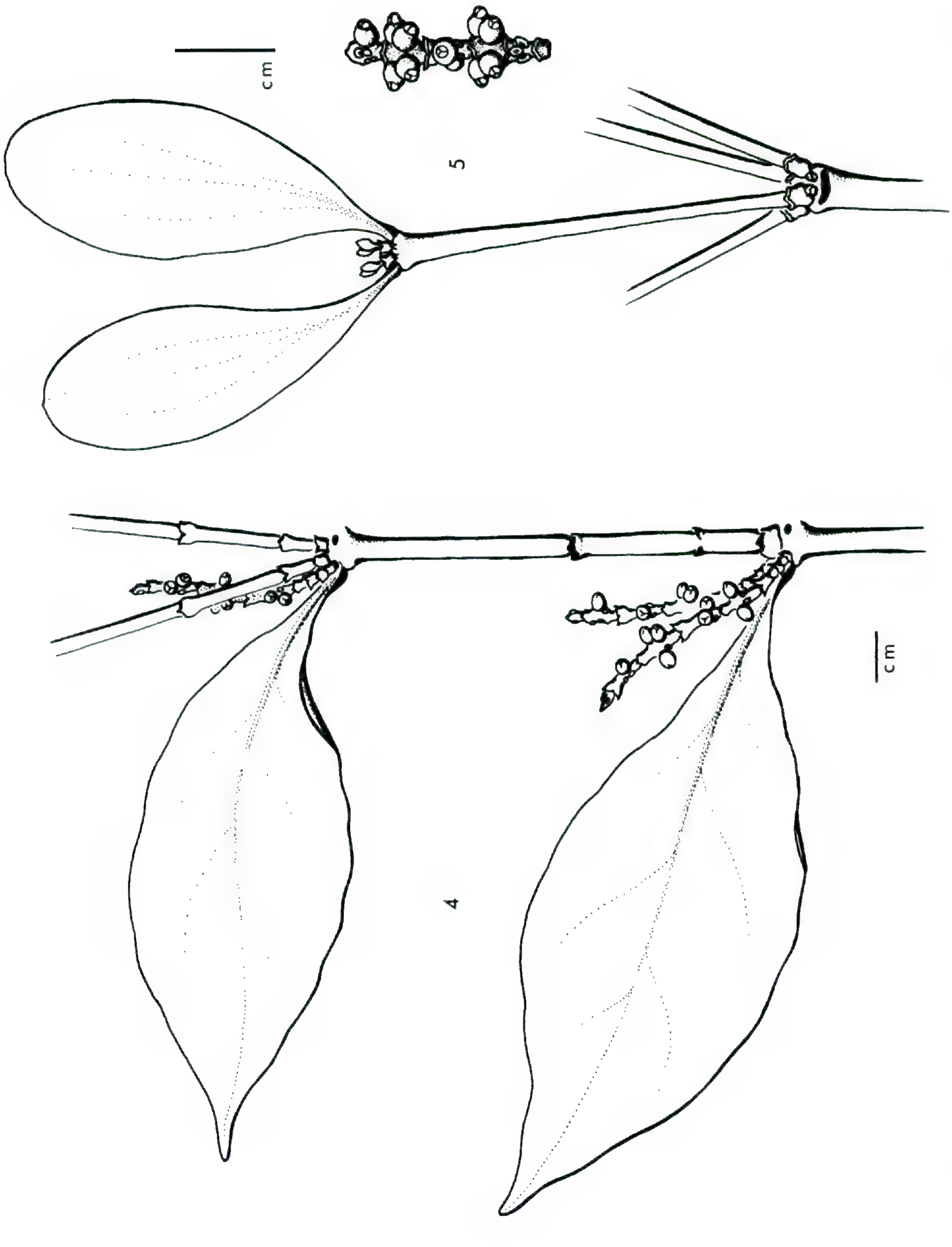
Rather sparsely and teretely branched plants; both percurrent and lateral branches with 3–4 pairs of sterile cataphylls, the branch tips sometimes aborting? *Leaves* rather thick, pinnately but obscurely veined except for the prominent midrib, broadly lanceolate, the apex attenuate, the petiole 10–15 mm long, the blade to 12 cm long and 5 cm wide. Probably *monoecious*. *Spike* ca. 45 mm long, with several short, sterile internodes and 4–5 fertile ones. *Flowers* in 1a and 1b (cf. Kuijt, 1936b) arrangement, the apical ones on many internodes apparently staminate, the others pistillate. *Fruit* ovate, 4 mm long, 3 mm wide, the petals closed.

This species seems to be almost exactly intermediate between *P. crassifolium* and *P. piperoides*. It shares the several intercalary cataphylls and proportions of leaves and spikes with the former, but these cataphylls bear no spikes, and leaf venation is not palmate as in *P. crassifolium*. *Phoradendron piperoides*, on the other hand, has only one pair of intercalary cataphylls, is smaller in leaf, petiole, and fruit, and its spikes bear more, but more spherical berries. The only other species with several sterile intercalary cataphylls is *P. woodsonii*. It differs in having leaves no more than half as long as the above, and in having correspondingly shorter internodes; more importantly, leaf venation is clearly palmate, and fruits are more spherical than elliptical. Our material does not seem to be represented in Trelease (1916).

PANAMÁ: Along El Llano Cartí-Tupile road, 12 mi above Pan-Am. Highway, primary forest, 200–500 m, *Liesner 1217* (MO, LEA).

19. **Phoradendron** sp.—FIG. 5.

A much branched, glabrous mistletoe with terete stems, some percurrent,



FIGURES 4–5.—4. *Phoradendron* sp. No. 18 (*Liesner 1217*).—5. *Phoradendron* sp. No.19 (*Dwyer, Crosby, Croat & Castillon 4340*).

others forking through apical abortion; percurrent branches lacking cataphylls; lateral branches with a single pair of white-margined cataphylls at the very base. *Leaves* elliptical, to 5 cm long and 2 cm wide, the apex obtuse, the base tapered into a short, flat petiole. Presumably *dioecious*; staminate plant or flowers not seen. *Pistillate spike* ca. 2 cm long, with a single, short sterile internode and 4–5 fertile ones; fertile bracts usually with 3 flowers in 1a arrangement. *Fruit* yellow, round, 2.5 mm wide, the petals closed, the floral cup conspicuous, the apex of the spike blunt.

The pistillate spike provisionally placed in *P. annulatum* in my Costa Rican revision (Kuijt, 1964) is more likely to belong with the present species, as it has fewer flowers per internode than the type. The Panamanian specimen cited below is clearly not related to *P. annulatum*. A peculiarity of this otherwise undistinguished mistletoe seems to be that spikes never develop in the axils of leaves, but only on older wood below. This feature and the terete stems immediately differentiate this species from *P. quadrangulare* with which it otherwise may be confused. The species is probably not included in Trelease's treatment (1916).

PANAMÁ: Road to Campana, near Pan-American Highway, roadside field, *Dwyer et al. 4340* (MO, LEA).

20. **Phoradendron** sp.—Fig. 6.

A glabrous, very stout and coarse plant, often forking through apical abortion; branches terete, to 1.5 cm thick below, the leaf-bearing ones 4–5 mm thick but to 10 mm thick at the leafy nodes; innovations of 2–5 internodes, all but the terminal node bearing pairs of large cataphylls, these more crowded toward the base; percurrent branches similar. Terminal node with extremely leathery elliptical *leaves*, the blade to 10 cm long and 13.5 cm wide, with a thick, callused margin and rounded apex, the base abruptly tapered into a massive petiole 3–5 mm wide, the venation palmate but usually obscure. *Dioecious*. *Pistillate spikes* to 5 cm long, consisting of several sterile, basal internodes and ca. 5 fertile ones with up to 18 flowers per internode in 3 series above each bract. *Staminate plants* not seen.

This very distinctive species has not been previously reported from Central America. It is related to *P. obliquum*, differing in having consistently more cataphylls on both innovations and inflorescences, in having symmetrical rather than falcate leaves, and in being apparently dioecious. The original description of *P. fendlerianum* Eichler (Eichler, 1868) appears to match our material; the type specimen was destroyed at Berlin-Dahlem, but its photograph survives in Trelease's monograph (1916: pl. 211b).

PANAMÁ: Cerro Jefe, 1000 m, *Mori et al. 3766* (MO, LEA); 2700–3000 ft, *Tyson et al. 3193* (MO), *3282* (MO), *4340* (MO, LEA). VERAGUAS: 3–4 km by road W of Santa Fé, 2500 ft, *Nee 11316* (MO, LEA).

8. PHTHIRUSA Eichler, Fl. Bras. 5(2): 52. 1868, non Mart. in Schult. & Schult., Syst. Veg. 7: 96. 1829.

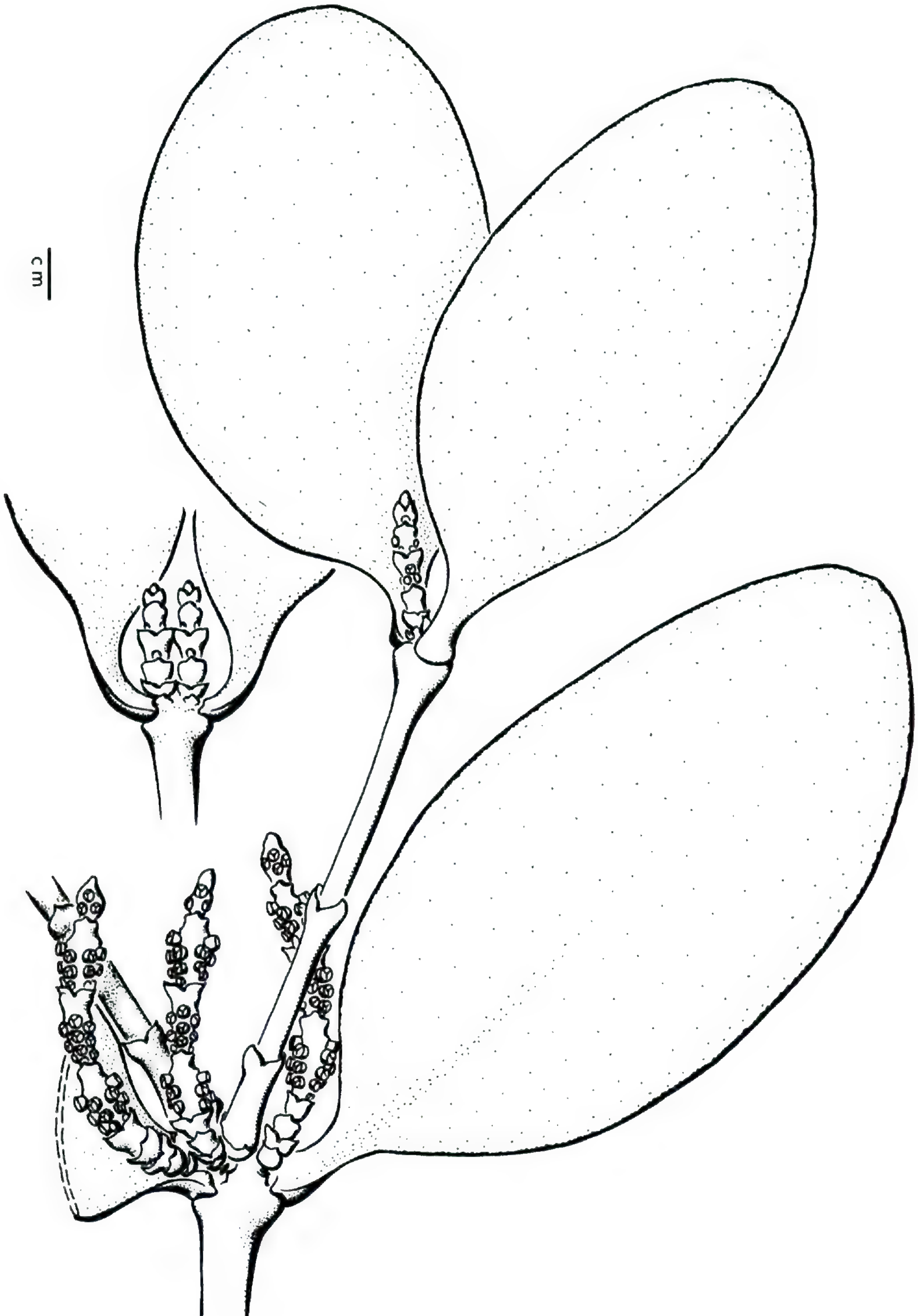


Figure 6.—*Phoradendron* sp. No. 20 (*Mori & Kallunki 3766*).

A rather large genus of uncertain distinction from *Struthanthus*, with two species in Panama. One of these is the type species, *P. pyrifolia*, the only *Phthirusa* north of Panama, reaching southern Mexico. In Rizzini's (1960) treatment no mention is made of the fact that many (if not most) species of *Phthirusa*, including the type species, have hermaphroditic flowers. However, there are some close relatives of *P. pyrifolia* which are dioecious, so that sex distribution alone cannot be used as a generic distinction. The other Panamanian species, *P. adunca*, is such a dioecious one. A third species mentioned by Rizzini (1960), *P. pittieri*, becomes a synonym of *Struthanthus leptostachyus*.

Critical literature: Rizzini, 1952; Kuijt, 1976b, Kuijt & Weberling, 1972.

a. Plants dioecious; flowers at least 4 mm long, pale yellow; inflorescence usually branched ..... 1. *P. adunca* (Meyer) Maguire
aa. Plants with the flowers hermaphroditic; flowers less than 3 mm long, dark wine red; inflorescence an unbranched spike or raceme ..... 2. *P. pyrifolia* (H.B.K.) Eichler

1. **Phthirusa adunca** (Meyer) Maguire, Bull. Torrey Bot. Club 75: 301. 1948.

This species reaches its northern limits in Panama, being very common in tropical South America.

2. **Phthirusa pyrifolia** (H.B.K.) Eichler, Fl. Bras. 5(2): 36. 1868.

While *P. adunca* develops roots on some branches, *P. pyrifolia* never does so. Both species, however, produce long roots with secondary haustoria from the base of the plant. The ovary of this species is solid, i.e., no ovarian cavity exists, the embryo sacs developing in the central parenchymatous tissues. Other anatomical peculiarities and a case for habitual autogamy in this mistletoe are presented by Kuijt & Weberling (1972). It is entirely possible that some of these unusual features are shared by related species or even the genera *Dendropomon* and *Oryctanthus*. Barlow & Wiens (1971) have found only tetraploids in Costa Rica, but only diploids in Ecuador, so that both chromosome races could conceivably occur in Panama.

9. Psittacanthus Mart., Flora 13: 106. 1830.

This is the only large-flowered genus in Central America with flowers which are at least partly red; the only other large, brightly colored mistletoe flowers in the area are the golden yellow ones of *Gaiadendron*. The genus is distributed from northern Mexico far into South America, with species on Jamaica, Martinique, and Dominica.

Critical literature: Eichler, 1868.

a. Leaves lacking petioles, the base clasping the stem; lower inside petals with vermiform marginal appendages ..... 3. *P. hamulifer* Kuijt
aa. Leaves petiolate; petals without vermiform marginal appendages.
  b. Inflorescence axillary or on older wood, the smallest unit a pair of flowers (diad); leaves mostly symmetrical.
    c. Leaves usually in whorls of 4 (sometimes paired); anthers nearly sessile, monomorphic, backed by a tuft of long, red hairs ..... 4. *P. nodosus* (Desr.) G. Don

cc. Leaves 2 or 3 per node, or irregularly spaced, rarely in whorls of 4; anthers on long filaments, dimorphic, hairless.
d. Flowers dilated at the base; leaves 7 cm long or more; petals not plicate ..... 1. *P. allenii* Woods. & Schery
dd. Flowers scarcely dilated at the base; leaves 6 cm long or less; petals plicate at the tip ..... 5. *P. pusillus* Kuijt
bb. Inflorescence terminal, the smallest unit a triad; leaves falcate or at least tending to be asymmetrical.
e. Mature buds 8–9 cm long, straight; leaves usually more than 6 cm wide ..... 6. *P. schiedeanus* (Cham. & Schlecht.) Blume
ee. Mature buds about 4 cm long, slightly curved; leaves usually less than 5 cm wide ..... 2. *P. calyculatus* (DC.) G. Don

1. **Psittacanthus allenii** Woods. & Schery, Ann. Missouri Bot. Gard. 27: 309. 1940.

P. lateriflorus Woods. & Schery, Ann. Missouri Bot. Gard. 27: 309. 1940.
P. scheryi Woods., Ann. Missouri Bot. Gard. 28: 426. 1941.

The ligular differences to separate the above are not thought to warrant any taxonomic recognition. *Psittacanthus allenii* is also extremely variable in its leaf shape and size. It has been collected in southern Mexico, Nicaragua, Costa Rica, and Panama. The closest relative of *P. allenii* seems to be *P. dilatatus* A. C. Smith, the latter having much thicker buds and 1–1.5 mm long, erect, strap-shaped ligules. Additionally, the stigma is situated below the anthers in *P. dilatatus*, but above the anthers in *P. allenii*. Another closely related species is *P. dichrous* (Mart.) Mart., of which authentic material has not been seen; the excellent illustration in the *Flora Brasiliensis* 5(2), *pl.* 8. 1868 shows a crenulate calyculus which *P. allenii* lacks. I have elsewhere remarked on the unusual fact that seedlings of *P. allenii* in some areas are dicotyledonous, in others polycotyledonous (Kuijt, 1970).

2. **Psittacanthus calyculatus** (DC.) G. Don, Gen. Syst. 3: 415. 1834.

P. chrismarii Urban, Bot. Jahrb. Syst. 24: 311. 1897.

Like *P. schiedeanus*, which it resembles somewhat, *P. calyculatus* ranges north to southern Mexico but, unlike the former species, it also occurs in Colombia and Venezuela. In the Costa Rica-Panama area, all known collections are from the Pacific slopes. While the two species are somewhat similar, the leaf and bud characters used in the key provide a clear separation.

3. **Psittacanthus hamulifer** Kuijt, sp. nov.—FIG. 7.

Planta sat robusta; caules paulus applanati nec costati; internodia usque ad 10 cm longa. Folia coriacea, usque ad 15 × 7 cm, pinnatinervia, ovata ad late lanceolata, basi cordata, amplexicaulia, apice acuta. Flores ut videtur in diadis; pedunculo pedicelloque circ. 5 mm longis, gracillimis; calyculus margine crenatus; petala 5 cm longa, alabastro anguste acutato, recta, laete aurantiaca, apice lutea; facies interior inferne (3 cm) seriebus marginalibus appendicum vermiformium duabus, supra eas stamina 1.5 cm longa inserta; antherae 4.5 mm longa, acumine aciformi 1 mm longo auctae, versatiles; stylus petala fere aequans; stigma breviter clavatum, papillosum.

Stems only very slightly flattened, the internodes to 10 cm long. *Leaves* coriaceous, to 15 cm long and 7 cm wide, pinnately veined with a very prominent

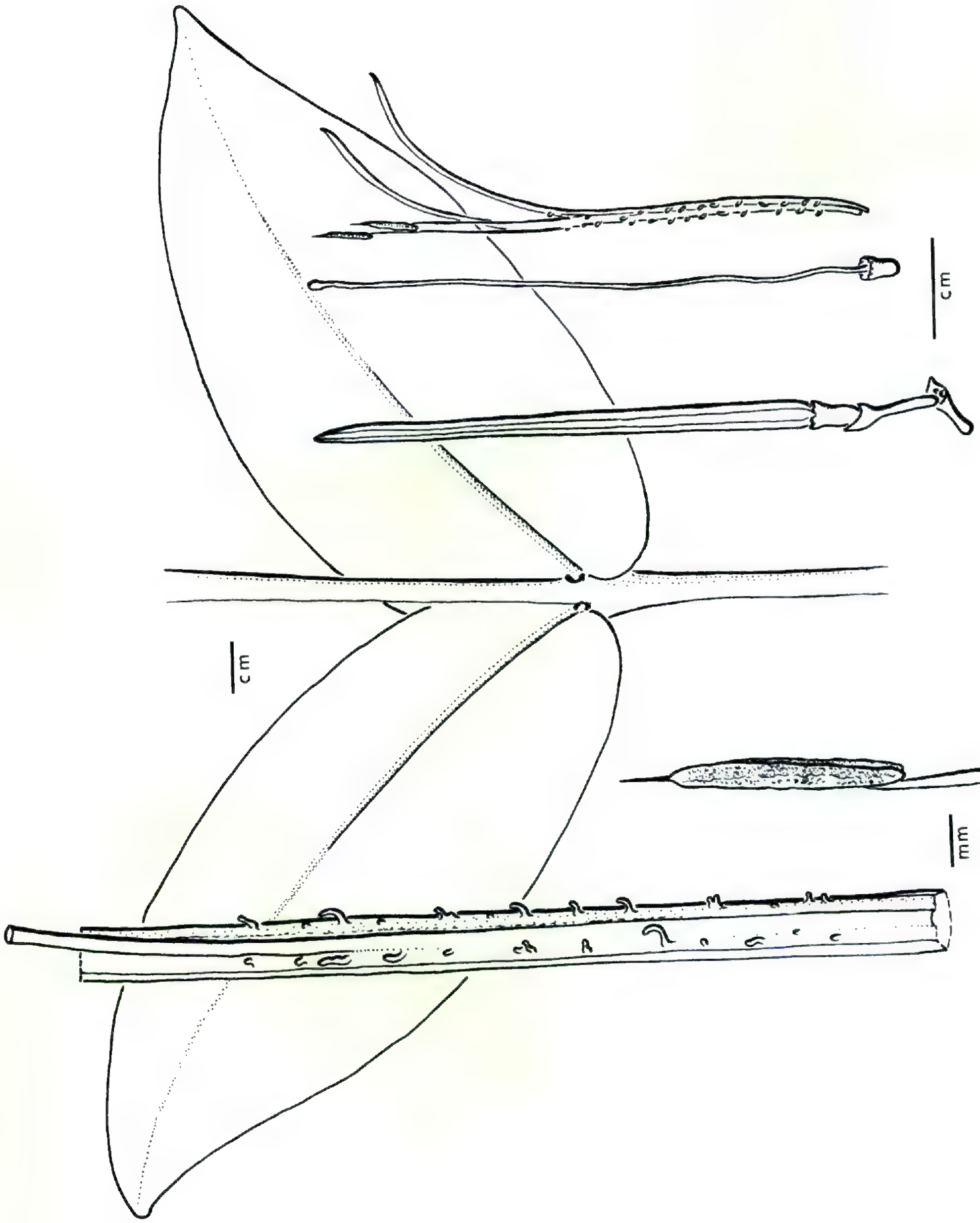


FIGURE 7.—*Psittacanthus hamulifer* Kuijt (*Duke & Elias 13681*), habit and floral details.

midvein, ovate to broadly lanceolate, the base cordate and clasping, the apex acute. *Flowers* (? only) in axillary positions, emerging from a "cushion" as in *Cladocolea* (cf. Kuijt, 1975), apparently in diads; peduncle about 5 mm; pedicel slightly longer, very slender, terminating in an oblique cup; petals 5 cm long, very narrowly pointed in the straight bud, bright orange with a yellow tip, with 2 rows of fleshy, hook-shaped, marginal, frequently paired appendages up to 0.5 mm long inside for the lowest 3 cm, at which point filaments attached; stamens 1.5 cm long, the anthers 4.5 mm, narrow, versatile, with a needlelike tip about 1 mm long, and of 2 different lengths; ovary 4 mm long, 3 mm wide at the irregularly scalloped calyculus; the style more or less straight, nearly the length of the flower, the stigma papillate, clavate. *Fruit* not seen.

This is an exceedingly interesting species because of its flower structure. The hooklike or vermiform appendages in what appears to be the tubular portion of the corolla may either function in holding the nectar (see the comparable internal corolla modifications in the African *Plicosepalus* and *Tapinostemma* as illustrated in Engler & Krause, 1935: figs. 70–71); or possibly, as their marginal position suggests, in linking the petals together. One other species (*Psittacanthus peronopetalus* Eichl.) has been reported with similar appendages (Eichler, 1868), but that species differs in having petioled leaves, a prominent ligule, apically diverging petals, and anthers lacking the needlelike tip.

TYPE: PANAMA. DARIÉN: On tree trunk in elfin forest, Cerro Pirre, cloud forest and/or mossy forest, 2500–4500 ft, *Duke & Elias 13681* (MO, holotype; DUKE, SCZ, isotypes).

4. **Psittacanthus nodosus** (Desr.) G. Don, Gen. Syst. 3: 417. 1834.—FIG. 8.

Loranthus nodosus Desr. in Lam., Encycl. 3: 601. 1809.
Desrousseauxia nodosa (Desr.) Van Tieghem, Bull. Soc. Bot. France 42: 358. 1895.
Aethanthus nodosus (Desr.) Engler, in Engler & Prantl, Nat. Pflanzenfam., Nachtr. 1: 136. 1897.

Stems terete, the nodes swollen, the internodes up to 12 cm long. *Leaves* in regular whorls of 4 (sometimes paired), to 8 cm long and 4 cm wide, rarely to three times this size (*Mori 8005*), ovate or obovate to broadly lanceolate, with a rough texture when dry. *Inflorescences* axillary, apparently consisting of several diads on a common, red peduncle. *Flowers* bright red or orange below, yellow above, 4–6 cm long in bud, the buds rounded at the apex, straight; calyx scarcely or not at all dilated at the base; anthers all inserted at the same height, 5 mm below the petal tips, nearly sessile and backed by a crescent of long reddish hairs; ovary 4 mm long, the style straight, with a small clavate stigma just beyond anthers. *Fruit* dark purple, ca. 9 mm long and 5 mm wide, with an inconspicuous calyculus.

The Central American material corresponds rather closely both to the original description and to the Jussieu type at Geneva, collected in Ecuador, notwithstanding the latter's more broadly ovate leaves. It should be noted, however, that there is no mention in the original description of hairs associated with the anthers.

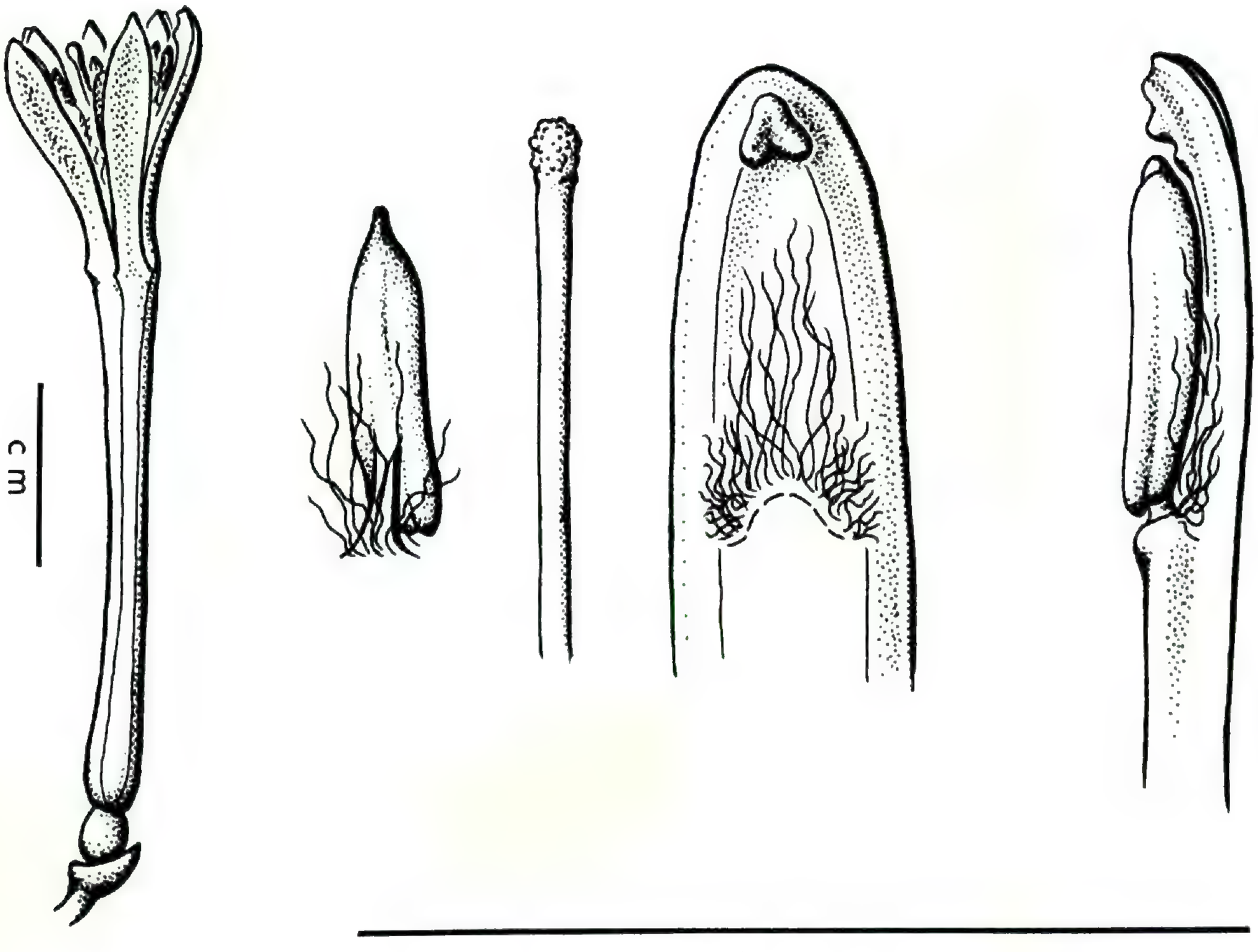


FIGURE 8.—*Psittacanthus nodosus* (Desr.) G. Don (*Luteyn & Foster 1122*). From left to right: flower; anther as seen from the back; tip of style; petal tip with anther removed (broken line); and anther and petal tip from the side.

The species is also known from Costa Rica where it was treated as an unidentified species (No. 29) of *Psittacanthus* (Kuijt, 1964).

A specimen of uncertain identity is *Gentry & Mori 14140* [Darién, central ridge of Cerro Tacarcuna massif, 1700–1800 m (MO)]. It resembles the present species except that the buds are slightly curved and unusually stout.

CHIRIQUÍ: Nubes, 5.5 km NW of Río Chiriquí Viejo, 2200 m, *Busey 661* (MO). Las Nubes, 5 km NW of Cerro Punta, 6000–6500 ft, *Mori & Bolten 7233* (DUKE); *Croat 26473* (MO, LEA). Río Chiriquí Viejo, 2 km NE of Guadelupe which is 2 km N of Cerro Punta, *Wilbur et al. 15368* (DUKE, MO). COCLÉ: El Valle de Antón: *Allen 2233* (US). El Valle de Antón, La Mesa, *Croat 14381* (MO). El Valle de Antón, Cerro Pilon, 2000 ft, *Dwyer & Correa 7995* (MO). COLÓN: La zona de Santa Rita, *Correa & Dressler 1816* (MO). DARIÉN: Colombia (Chocó)-Panama (Darién) border, slopes of Serrania del Darién E of Ungía, 300–1300 m, *Gentry et al. 16774* (MO). PANAMÁ: 8 km above Goofy Lake on road to Cerro Jefe, *Correa & Dressler 477* (MO). 1 mi beyond La Eneida, Cerro Jefe, *Correa & Dressler 971* (MO). Cerro Jefe, *D'Arcy & D'Arcy 6248* (MO); *Dwyer & Gauger 7334* (MO); *Dwyer & Hayden 8088* (MO); *Gentry 6166* (MO); *Gentry & Dwyer 5538* (MO). Near La Eneida, 100 m, *Luteyn & Foster 1122* (DUKE, MO). Cerro Jefe, 1000 m, *Mori 8005* (MO); *Mori & Kallunki 3631* (MO). Above Goofy Lake on road to Cerro Jefe, *Weaver & Foster 1496* (DUKE). VERAGUAS: 7 km NW on road to Santa Fé, *D'Arcy 10285* (MO). 3–5 mi N of Santa Fé, 500–1000 m, *Gentry 2956* (MO). N of Santa Fé, *Mori & Kallunki 2599* (MO). 3–4 km W of Santa Fé, 2500 ft, *Nee 11318, 11320* (both MO).

5. **Psittacanthus pusillus** Kuijt, sp. nov.—FIG. 9.

Frutex parvus, gracilis; caules teretes; flores bini axillares, innovationibus ex internodiis 1–4 constantibus insidentes. Folia bina vel fere, elliptica ad late lanceolata, usque ad 6 × 2.5 cm, petiolis 1–3 mm longis. Diadae singulae in axillis; pedicelli 8–10 mm longi, cupula ampliata terminati. Flos 30–40 mm longus; corolla 27–30 mm longa, recta vel paulum curvata, aurantiaca, apice luteo vel viridescente; petala apice conspicue plicata, ligula minuta; stamina dimorpha, ante anthesim haud imbricata.

A small and slender species, the stems terete and smooth with fine longitudinal cracks in age, ca. 2 mm thick when flower bearing. *Leaves* paired but sometimes irregularly spaced, elliptical to broadly lanceolate, to 6 cm long and 2.5 cm wide, the petiole 1 mm thick and 1–3 mm long, the apex rounded, the base tapering into the petiole, only the midvein visible when dry. *Flowers* axillary only, only on innovations 1–4 internodes long, in diads (rarely a triad), these 1 per leaf axil, 3–4 cm long; peduncles 3–7 mm long, ca. 1 mm thick, often consisting of 2 internodes lacking leaves, emerging from a craterlike axillary rim of brown tissue; pedicels 8–10 mm long, ca. 1 mm thick, terminating in a flaring cuplike structure 4 mm wide; corolla 27–30 mm long; the corolla tube straight or slightly curved, 3–4 mm wide at the rounded tip, scarcely dilated below, said to be orange with yellow or with a greenish apex, the petals conspicuously plicate at the tip, 6, the ligule very small; stamens dimorphic, slightly shorter than the petals, the anthers versatile, 3 mm long, not overlapping in bud, the filaments 12–15 mm long; ovary globose, ca. 3 mm in diameter, the calyculus smooth, the style slender, 25 mm long, the stigma small, elliptical, with finely papillate surface. *Fruit* unknown.

The closest relative of this species may be the Ecuadorian *P. obovatus* (Benth.) Eichler which is similarly small leaved but has terminal inflorescences. I know of no other *Psittacanthus* flowering by means of such leafy innovations.

TYPE: PANAMA. PANAMÁ: In forest, about 1 mi upstream from Frizzel's Finca Indio, on slopes of Cerro Jefe, *Foster & Kennedy 1863* (DUKE).

Other material seen: PANAMÁ: Cerro Jefe, 2.5 mi beyond Finca Indio, *Gentry 2108* (MO). Road past Cerro Azul, 20 km from junction with road through Tocumen, *Mori & Kallunki 2192* (MO). 8 km above Goofy Lake on road to Cerro Jefe, *Weaver & Foster 1499* (DUKE).

6. **Psittacanthus schiedeanus** (Cham. & Schlecht.) Blume in Schult. & Schult., Syst. Veg. 7: 1730. 1830.

10. STRUTHANTHUS Mart., Flora 13: 102. 1830.

This is perhaps the most difficult genus in neotropical Loranthaceae, at least in part because it seems to be polyphyletic (Kuijt, 1975). Especially the plants in the *marginatus-quercicola* complex are often difficult to identify. In this regard, the present treatment is little more than an extrapolation of my Costa Rican treatment (1964).

Critical literature: Eichler, 1868; Kuijt, 1964.

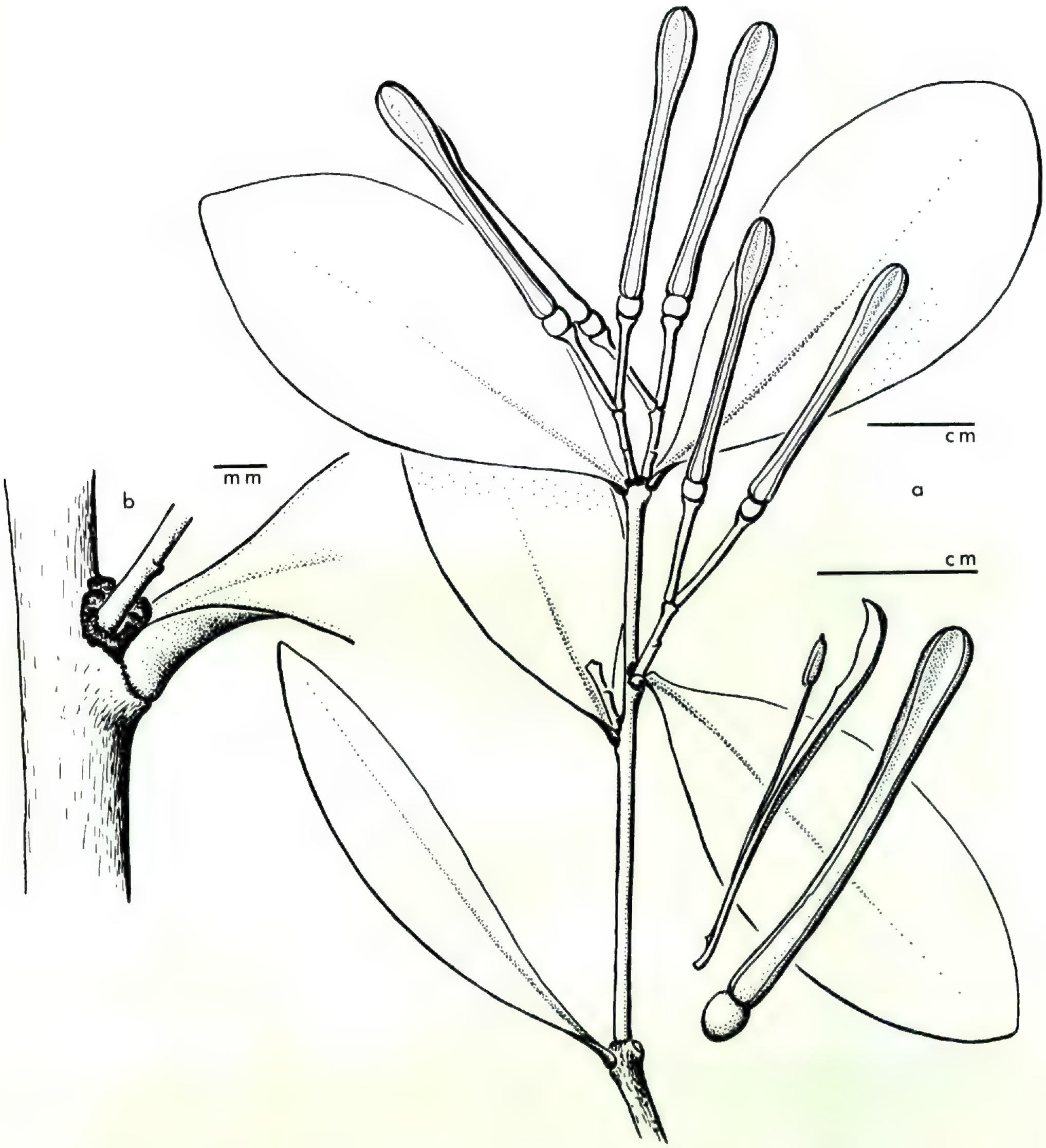


FIGURE 9.—*Psittacanthus pusillus* Kuijt, type (*Foster & Kennedy 1863*).—a. Habit and floral details.—b. Axillary cushion at base of diad.

a. Each flower supported by 1 bract and 2 bracteoles, these monads paired along the raceme axis ..... 5. *S. panamensis* (Rizz.) Barlow & Wiens

aa. Flowers in triads, these with 1 bract and 2 bracteoles and paired along the raceme axis.

b. Stem (often also inflorescence axis) dotted with large lenticels; inflorescence subtended by persistent papery bracts ..... 2. *S. leptostachyus* (H.B.K.) G. Don

bb. Stems lacking obvious lenticels; inflorescence without persistent papery bracts.

c. Bracteoles of female flowers stout and persistent.

d. Mature fruit dark blue, more than 7 mm long; some young leaves prehensile ..... 7. *S. rotundatus* Rizz.

dd. Mature fruit reddish orange, less than 7 mm long; leaves never prehensile ..... 6. *S. quercicola* (Cham. & Schlecht.) Blume

cc. Bracteoles of female flowers delicate and deciduous.
e. Young leaves prehensile, on somewhat quadrangular stems; fruit blue when mature, at least 1 cm long, on swollen pedicel with lenticels ..... 4. S. *orbicularis* (H.B.K.) Blume
ee. Young leaves not prehensile, on terete stems; fruit reddish to yellow, less than 1 cm long, the pedicel not conspicuously swollen.
f. Inflorescence axis very delicate, sometimes with no more than 4 triads; triad peduncle 2–3 mm long; fruit 5 mm long, 3 mm wide; leaves commonly 3 or more times as long as wide, with a very attenuate apex ..... 1. S. aff. *dichotrianthus* Eichler
ff. Inflorescence axis not particularly delicate, always with more than 6 triads; triad peduncle 2 mm long or less; fruit 7 mm long, 5 mm wide; leaves usually less than 3 times as long as broad, the apex not or scarcely attenuate ..... 3. S. *marginatus* (Desr.) Blume

1. **Struthanthus** aff. **dichotrianthus** Eichler, Fl. Bras. 5(2): 75. 1868.

Scandent *shrub* with terete stems and stem-roots. *Leaves* paired, thin, 7–11 cm long, 1.5–4.5 cm wide, including a 2–5 mm, tapering petiole, the blade ovate to lanceolate, with a slender, attenuate tip. *Inflorescence* very slender, 1 or 2 per axil; peduncle up to 1 cm long, with 2 or 4(–10) triads each on peduncle of similar length. *Flowers* not seen. *Fruit* oblong to spherical, to 4 mm long and 5 mm wide, yellow to bright orange, the median one sessile, the lateral ones on pedicels nearly 2 mm long.

It is possible that this material corresponds to what has been referred to as *Struthanthus* No. 37 (Kuijt, 1964); certainly Fig. 37 in that article illustrates the habit of the Panamanian material. The D'Arcy collection is very narrow-leaved, and its inflorescences are also more elongate than the Coclé material. Finally the Luteyn collection has up to 10 triad pairs per inflorescence. Whether all this material [plus the *von Wedel 1287* (GH) mentioned in Kuijt (1964: 301)] constitutes a single variable species, or whether all are variants of S. *marginatus* remains an open question.

BOCAS DEL TORO: Between Buena Vista coffee finca and Cerro Pilon, *Kirkbride & Duke 709* (LEA, MO). COCLÉ: Foothills of Cerro Pilon, near El Valle, 900 m, *Duke & Correa 14673* (MO). Cerro Caracoral, 900 m, *Duke & Dwyer 15131* (MO). La Mesa, above El Valle, *Dwyer 11862* (LEA, MO). Foot of Cerro Pilon, above El Valle de Antón, 2000 ft, *Porter et al. 4409* (LEA, MO). VERAGUAS: 7 km NW on road to Santa Fé, *D'Arcy 10280* (MO). ? NE slopes of Cerro Delgadito, just NW of Cerro Tuté, S of town of Santa Fé, 1000 m, *Luteyn 4024* (DUKE).

2. **Struthanthus leptostachyus** (H.B.K.) G. Don, Gen. Syst. 3: 411. 1834.

Loranthus leptostachyus H.B.K., Nov. Gen. Sp. Pl. 3:440. 1818.
L. pyrifolius Willd. in Schult & Schult., Syst. Veg. 7: 1647. 1830, non H.B.K.
Peristethium leptostachyum (H.B.K.) Van Tieghem, Bull. Soc. Bot. France 42: 175. 1895.
Phthirusa pittieri Krause, Repert. Spec. Nov. Regni Veg. 15: 441. 1919.

This species is not to be confused with: *Viscum leptostachyum* Spreng. in DC., Prodr. 4: 280. 1830 = *Dendrophthora leptostachya* (Spreng.) Eichler, Fl. Bras. 5(2): 104. 1868 = *Phoradendron leptostachyum* (Spreng.) Index Kew. 3: 502. 1894 = *Dendrophthora flagelliformis* (Lam.) Krug & Urban.

This common species has frequently been referred to as S. *polystachyus* (Ruiz & Pavón) Blume, as in Rizzini's (1960) and my own (Kuijt, 1964) treatments.

The type of *Loranthus polystachyus* Ruiz & Pavón, however, has leaves which are consistently different in shape from Central American material, which almost certainly is specifically distinct. In Central America this mistletoe is unique in having a cluster of persistent, papery scale leaves which invests the base of each inflorescence, and in the fact that the tip of the inflorescence, instead of the usual triads of flowers, has single flowers, and even terminates in a single flower (Kuijt, 1964). On the basis of the scale leaves (and supposed hermaphroditic flowers: the flowers are in reality unisexual, the plants dioecious as elsewhere in *Struthanthus*), Van Tieghem (1895) erected the monotypic genus *Peristethium*. *Struthanthus leptostachyus* appears to be closely related to *Cladocolea archeri* (A. C. Smith) Kuijt, confronting us with a nettly taxonomic problem at the generic level (Kuijt, 1975). In the limited sense, this species ranges from Costa Rica as far as Ecuador.

The collection *Tyson et al.* 3233 [Panamá, Cerro Jefe in *Clusia* forest, 2700–3000 ft (MO)] is a very small-leaved specimen. Its relationship to *S. leptostachyus* is clear, but it may represent an undescribed species.

3. **Struthanthus marginatus** (Desr.) Blume in Schult. & Schult., Syst. Veg. 7: 1731. 1830.

Equivalence of Central American *S. marginatus* to the type material from eastern Brazil is by no means certain, but cannot be ascertained at this time.

4. **Struthanthus orbicularis** (H.B.K.) Blume in Schult. & Schult., Syst. Veg. 7: 1731. 1830.

This is one of several species of *Struthanthus* which uses its young leaves in a prehensile fashion. It is not synonymous with *S. rotundatus* as previously indicated (Kuijt, 1964). This species ranges from southern Mexico into Brazil and Peru. See comments under *S. rotundatus*.

5. **Struthanthus panamensis** (Rizz.) Barlow & Wiens, Brittonia 25: 39. 1973.

Phrygilanthus panamensis Rizz., Ann. Missouri Bot. Gard. 47: 270. 1960.

This enigmatic species had earlier been thought to be related to *Phrygilanthus palmeri* Watson which, however, was relegated to *Psittacanthus* by Barlow & Wiens (1973). The indicated affinity is out of the question, but the generic status of the species remains uncertain. It might be added that the genus *Phrygilanthus* has been totally dissolved for nomenclatural and other taxonomic reasons (Barlow & Wiens, 1973). The present species may be out of place in *Struthanthus* because of its apparently hermaphroditic flowers and the one-flowered inflorescence unit rather than the triads of other species of *Struthanthus*.

CHIRIQUÍ: Bajo Chorro, Boquete District, 1800 m, *Davidson 431* (US, holotype; A, F, isotypes); *Davidson* 392 (US). NE ridge leading to Cerro Horqueta, 1800–1900 m, *Luteyn 3786* (DUKE). Cerro Colorado, 50 km N of San Felix, 1200–1500 m, *Mori & Dressler* 7825 (MO). Chiriquí Viejo ca. 2 mi NE of Cerro Punta, 7000 ft, *Wilbur & Teeri 13109* (DUKE).

6. **Struthanthus quercicola** (Cham. & Schlecht.) Blume in Schult. & Schult., Syst. Veg. 7: 1731. 1830.

Scandent green *shrub* with epicortical roots, the stems smooth but often somewhat ridged when young, grey. *Leaves* petiolate, ca. 10 cm long and 4 cm wide, ovate, usually thin, the apex attenuate. *Inflorescences* 1–6 per axil, to 50 cm long, then with about 36 flowers in triads with 2–3 mm long stalks; median flower sessile, the lateral ones nearly so; bracts persistent in pistillate flowers, becoming somewhat fleshy in fruit, deciduous at least in some staminate flowers. *Flowers* light green or yellowish, 4 mm across when expanded; petals 2 mm long; stamens shorter, dimorphic, the anthers brownish yellow; style 2 mm long. *Fruit* an orange berry, elliptical to ovoid, 4 mm long, 6 mm wide, supported by somewhat swollen, short pedicels (lateral flowers) or sessile (median flower).

The species is based on a type from Mexico (Jalapa) and is especially common in Costa Rica (Kuijt, 1964). Some of the collections cited earlier (Rizzini, 1960) under *S. marginatus* in reality belong here. Only some representative specimens are cited below.

BOCAS DEL TORO: Along RR near station at Milla 10, *Croat 16339* (LEA, MO). CHIRIQUÍ: Along Río Chiriquí Viejo just above Guadelupe, *Croat 16036* (LEA, MO). E slope of Volcan de Chiriquí (Baru), 2200–2300 m, *Davidse et al. 10185* (LEA, MO). Cerro Respinga, E of town of Cerro Punta, 2000–2500 m, *Gentry 5944* (LEA, MO). W side of Cerro Horqueta, 1700–1800 m, *Luteyn 3759* (DUKE). 2 km W of La Garita about 3 km WNW of Cerro Punta, 2000 m, *Wilbur et al. 15286* (DUKE). Ca. 6 mi NW of Boquete, 1450 m, *Wilbur et al. 11970* (DUKE). DARIÉN: S slope of westernmost peak of Cerro Tacarcuna massif, 1100–1300 m, *Gentry et al. 16874* (MO). LOS SANTOS: 4 mi S of Limón, *Correa et al. 68* (MO). VERAGUAS: N of Santa Fé, on property of Escuela Agrícola Alto de Piedra, *Mori & Kallunki 2606* (LEA, MO).

7. **Struthanthus rotundatus** Rizz., Revista Brasil. Biol. 10: 401. 1950.

This is a clearly distinct species which I erroneously referred to *S. orbicularis* (Kuijt, 1964), to which it is nevertheless closely related. The young leaves are prehensile as in *S. orbicularis*. The two species may be separated in that *S. rotundatus* is generally larger in habit and inflorescences; this species has conspicuous floral bracts and bracteoles which persist in fruit, while those of *S. orbicularis* are small and caducous; the fruiting peduncles of *S. orbicularis* are greatly swollen and show large lenticels, those of *S. rotundatus* are not so swollen and lack lenticels. Finally, the mature fruits of *S. rotundatus* are said to be orange while those of *S. orbicularis*, even though passing through a brick red phase, are dark blue when ripe. The present species was originally described from Brazil.

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NOTES

AN ADDITIONAL SPECIES, A NEW SECTION, AND AN EARLIER EPITHET IN *CIENFUEGOSIA* CAV. (MALVACEAE)

When Kearney (1955) described *Hibiscus hitchcockii* Ulbrich ex Kearney on the basis of two specimens from Ecuador and Peru, he compared it to *H. sororius* L.f. and provided a table distinguishing the two species. The *Flora of Peru* (Macbride, 1956) repeated Kearney's description in essence and offered no additional details. In the course of studying loans of *Hibiscus* L. from European herbaria, I encountered two previously unidentified collections of *H. hitchcockii*. A close examination of these and the two collections upon which the original description was based has convinced me that this species is not closely related to *H. sororius* and that in fact it is not even a *Hibiscus*. In *H. hitchcockii* the embryo is conduplicate and there are "gossypol glands" on the petals and young stems. These features together are diagnostic of the tribe Gossypieae Alef. (cf. Fryxell, 1968), but neither is found in *H. sororius* nor in the tribe Hibisceae Reichenb. as a whole. Moreover, as in many Gossypieae, the style in *H. hitchcockii* has very short branches and the stigmas are clavate-decurrent, whereas in the Hibisceae the style branches are nearly always longer and, as far as is known, the stigmas are always capitate.

Of the eight genera which together form the tribe Gossypieae, the genus *Cienfuegosia* Cav. best accommodates *H. hitchcockii* on the basis of the following combination of characters: New World tropical distribution, shrubby habit, 8- to 9-merous involucre, pluriovulate carpels, and epunctate embryo. An amplified description is provided here which incorporates details of a larger sample of specimens and introduces features of the mature fruits and seeds which were not available to Kearney.

Cienfuegosia hitchcockii (Ulbrich ex Kearney) O. Blanchard, comb. nov.

Hibiscus hitchcockii Ulbrich ex Kearney, Leafl. W. Bot. 7: 271. 1955.

Shrubs or subshrubs to 2 m tall, the new growth moderately to densely stellate-tomentellous, blackish-punctate beneath the hairs. Leaf blades broadly ovate to suborbicular in outline, palmately nerved, mostly 5–11 cm long, 4.5–10.5 cm broad, shallowly 3- or 5-lobed, the lobes broadly and shallowly rounded or broadly triangular and broadly acute at the apex, the margin unevenly and usually shallowly crenate to crenate-serrate, the base truncate to broadly cordate, the nerves beneath lacking nectaries, the surface velvety-tomentose below, more sparingly pubescent above; petioles short, 1.8–4.0 cm long, ⅓–½ the length of the blade; stipules linear-subulate, 6–9 mm long, subpersistent. Flowers solitary in the axils of the upper leaves, usually collateral with a vegetative bud; peduncles at flowering 3.5–9.5 cm long, 1–2 mm in diameter, expanding gradually beginning in the upper third, to 2.5–3 mm wide at the base of the involucre, unarticulated. Involucre lacking nectaries at the base, the bracts 8 or 9, 12–18 mm long, 6–9

mm broad, spatulate-ovate, acute or short-acuminate, somewhat conduplicate, especially toward the base, ⅔ to nearly equalling the length of the calyx, enlarged somewhat in fruit, weakly 5-nerved, tomentose dorsally, sparingly stellate-pubescent ventrally. Calyx 16–22 mm long at flowering, to 26 mm in fruit, lobed to within 3–4 mm of the base, the segments erect, narrowly triangular, acute to acuminate, 3-(or 5-)nerved, the outermost pair of nerves obscure, all stellate tomentose, the intervals between them less so. Corolla broadly funnelform, 4.5–7.0 cm long, the petals overlapping nearly to their tips, more than twice the length of the calyx, rose, densely but minutely blackish-punctate throughout, farinose with coarse, short-armed stellate hairs dorsally where exposed in bud. Staminal column short, straight, about 1.4 cm long; anthers about 1 mm long. Style 3–4 cm long, more than twice the length of the staminal column, ⅔ the length of the corolla, 5-branched, the branches 2–3 mm long; stigmas broadly clavate-decurrent. Fruit ovoidal, apiculate, 5-valved, 18–25 mm long, the apiculum stiff, attenuate, nearly reaching the tips of the calyx, the surface pusticulose-rugose, reddish brown to dark brown; valves orange on the inner walls, ciliate on the margins within, the hairs long and often twisted. Seeds several per locule, turbinate-reniform, 4.5–5.0 mm long, lanate, the hairs grayish yellow; embryo conduplicate, the cotyledons enclosing the mesocotyl, epuncate.

TYPE: ECUADOR. PROV. GUAYAS: Oil camp between Guayaquil and Salinas, lat. 2° S, 0–1,000 m, 21–24 June 1923, *Hitchcock 20114* (GH, holotype; NY, US, isotypes).

Additional specimens examined: ECUADOR. Bahia de Caraquez, Mai und Juni 1901, *Lehmann B.T. 141* (L, NY).

PERU. PROV. HUANCABAMBA: Dept. Piura, between Canchaque and Serran about 5° S, 450 m, 6 Apr. 1939, *Stork* (*Goodspeed Exped. 11421*) (GH). Without specific locality or date, *Pavon s.n.* (G, P).

Cienfuegosia hitchcockii recombines characteristics of the New World sections *Cienfuegosia* and *Robustia* Fryx. (cf. Fryxell, 1969). This and the unique form of the involucral bracts call for the establishment of a new, monotypic section.

Cienfuegosia sect. **Spathulata** O. Blanchard, sect. nov.

Folia nectariis carentia, 3- vel 5-lobata, lobis non profundis. Stipulae linearo-subulatae. Flores in axillis foliorum superiorum solitarii, pedunculis non articulatis. Involucrum basi nectariis carens, bracteis 8 vel 9, spathulato-obovatis, aliquantum conduplicatis. Petala punctulata. Stylus 5-ramosus, ramis brevissimis, stigmatibus clavato-decurrentibus. Capsulae valvae intus in marginibus ciliatae.

Leaves lacking nectaries, 3- or 5-lobed, the lobes shallow. Stipules linear-subulate. Flowers solitary in the axils of the upper leaves, the peduncles not jointed. Involucre lacking nectaries at the base, the bracts 8 or 9, spatulate-obovate, somewhat conduplicate. Petals punctulate. Style 5-branched, the branches very short, the stigmas clavate-decurrent. Valves of the capsules ciliate on the margins within.

Type species: *Cienfuegosia hitchcockii* (Ulbrich ex Kearney) O. Blanchard

A second little-known *Hibiscus* to come to my attention from a European

loan is *H. glabrifolius* St.-Hilaire & Naudin, which was published in 1842. Gürke (1892) treated this species in *Flora Brasiliensis*, but he was unable to place it in any of the known sections of the genus *Hibiscus*. Hochreutiner (1900), in his revision of *Hibiscus*, included *H. glabrifolius* only in an addendum and simply mentioned that he was unable to locate the type at Paris. It is clear that both authors relied solely on the original description and that they had no specimens at their disposal.

The type specimen, which is indeed at P, was obtained originally by Gaudichaud from the "Herbier Impérial" of Brazil, according to the label. It conforms in essentially every detail to the original description of *Cienfuegosia cuyabensis* Pilger, which appeared in 1902, and to the later redescription of that species by Fryxell (1969) in his revision of *Cienfuegosia*. Since the St.-Hilaire & Naudin epithet is much the earlier of the two, a new combination is necessary.

Cienfuegosia glabrifolia (St.-Hilaire & Naudin) O. Blanchard, comb. nov.

Hibiscus glabrifolius St.-Hilaire & Naudin, Ann. Sci. Nat. Bot., sér. 2, 18: 40. 1842. TYPE: Brazil, Province de Matto Grosso, date and collector unknown (P, holotype).

Cienfuegosia cuyabensis Pilger, Bot. Jahrb. Syst. 30: 171. 1902. TYPE: Brazil, Mattogrosso, im Serrado bei Cuyabá, kreichend an trocknen, freien, sandigen Stellen, die Zweige dem Boden anliegend, Mar. 1899, *Pilger 289* (B, holotype, destroyed; photo at F). Brazil, Mato Grosso, Cuyabá, 9 June 1962, *Malme 1666* (S, neotype).

Other than the types cited above, the only collection of which I am aware is *Irwin & Soderstrom 6742*, Mato Grosso, ca. 70 km N of Xavantina, 10 Oct. 1964 (NY). Since all four of the known collections are from the state of Mato Grosso in Brazil, *C. glabrifolia* appears to be of rather limited distribution.

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NEW AND NOTEWORTHY ASTERACEAE FROM PANAMA

Neomirandea folsomiana Dillon & D'Arcy, sp. nov.—FIG. 1.

Herba ad 1 m alta, foliis oppositis 15 cm longis, 13 cm latisque acute prominenterque lobatis molliter pubescentibus. Inflorescentia paniculata florida, pedunculo pubescenti, pedicellis interdum bracteas medias lineares ciliates angustas ferentibus. Capita ca. 9 mm longa, in-

volucro basim bracteis linearis ciliatus subtenta, bracteis involucri deciduis obtusis vel rotundis in ca. 4 seriatis imbricatis, corollis dilute purpureis tubularis glabris 6 mm longis laciniis ca. 1 mm longis ciliolatis, lobis stylorum sursum incrassatis.

Robust, tomentose *herb*, to 1 m tall; stems tomentose with weak, spreading, brownish trichomes, perhaps glabrescent. *Leaves* broadly ovate, to 15 cm long, 13 cm wide, truncate, saliently lobed, the lobes acuminate, the sinuses rounded, the margin with low, numerous, glabrous teeth, slightly discolorous, drying darker above, both sides softly tomentose with weak, browning trichomes, prominently 3-nerved from just above the base, each nerve with ca. 2 major lateral, arcuate veins on each side and numerous lesser lateral veins, conspicuously elevated and appearing broad beneath, slightly elevated and appearing narrow above; petiole stout, tomentose, darker above, ca. 6 cm long. *Inflorescence* a many-flowered panicle to 35 cm tall; peduncle stout, straight, erect and tomentose to the first node, ternately and dichotomously branched, the divisions slender; pedicles slender, 3–15 mm long, tomentulose, sometimes subtended by 1–2 bracts or with a pair along the length. *Heads* with the involucre cylindrical, ca. 6 mm long, ca. 4 mm wide, ultimately deciduous, 4- to 5-seriate; phyllaries strongly graduated, imbricate, somewhat appressed, the calycerate bracts ca. 3 mm long, narrow, ciliate, the outer phyllaries ovate, ca. 3 mm long, glandular, ciliate, brown, the inner phyllaries oblong to narrowly lanceolate, ca. 6 mm long, the apices and keels with a distinct, brownish area, striate, ciliolate; receptacle convex, sparsely pilose; corolla pale, vivid purple, ca. 6 mm long, tubular, the lobes ca. 1 mm long, minutely ciliolate; anthers ca. 1.5 mm long, the appendages ca. 0.2 mm long, as broad as long, obtuse; style branches ca. 5 mm long, expanded distally. *Achenes* prismatic, black, ca. 3 mm long, strongly 5-angled, the carpopodium larger than the achene base, annular, contrasting tan; pappus of ca. 4 slender, scabrous, persistent bristles, ca. 5 mm long, brownish yellow.

TYPE: PANAMA. COCLÉ: Just below summit, El Petroso, *D'Arcy 11330* (MO, holotype; K, PMA, US, isotypes).

This species is distinctive in its sharply lobed, felty leaves which represent a considerable expansion of the pubescence character known to date in *Neomirandea*. When in flower, the style branches are the same color as the corolla and showy. The short, narrow, ciliate, pedicellate and calycerate bracts are distinctive, and are found also in the closely related *N. angularis* (B. L. Rob.) King & Rob. of Costa Rica. These two species share similar leaf shape, inflorescences, capitula, and habitat preferences. Less closely related are *N. burgeri* King & Rob., *N. grosvenorii* King & Rob., and *N. guevarii* King & Rob. all from Costa Rica, and *N. panamensis* King & Rob. from Bocas del Toro, Panama. All are large perennial herbs, with large deltoid to aceriform leaves, broad corymbose panicles, and phyllaries imbricate in 4–5 series, broadly ovate to oblong, and usually ciliate. On old pedicels, all phyllaries are deciduous, leaving only a minute, pilose receptacular knob.

Neomirandea folsomiana was found in the cloud forest on El Petroso which is just north of El Copey. This area was recently discovered botanically by James Phillip Folsom, collector at the Missouri Botanical Garden facility at Summit and Ancón in the Canal Zone. Plants were frequent along a new road

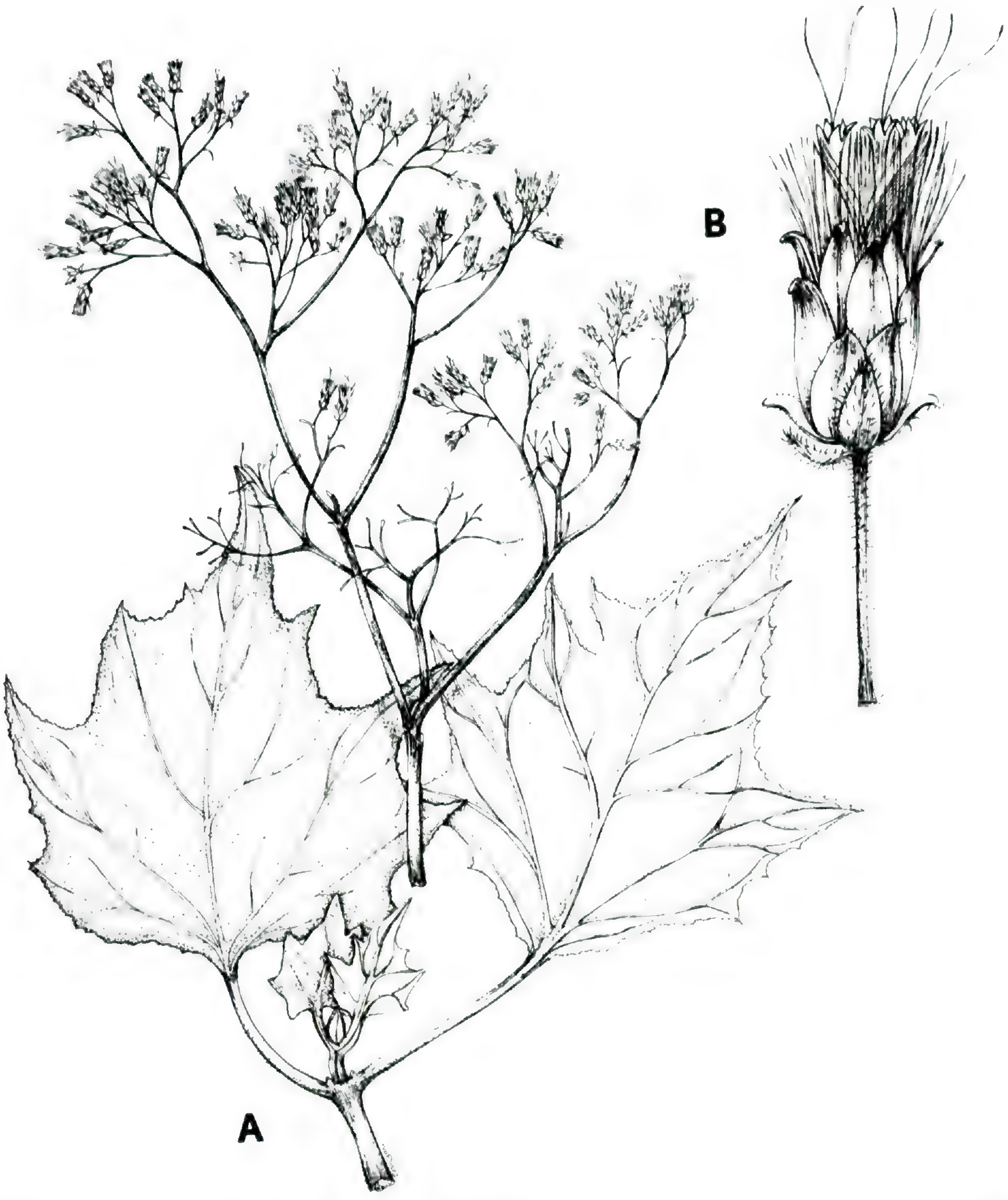

FIGURE 1. *Neomirandea folsomiana* Dillon & D'Arcy.—A. Habit (×⅖).—B. Head (×4⅕). [After *D'Arcy 11330* (MO.)]

leading to the summit and they formed large patches of color amongst the other vegetation. A recent photograph of this species taken by Barry Hammel, the succeeding collector at the Missouri Botanical Garden facility, aided in the above description.

Liabum biattenuatum Rusby, Descr. S. Amer. Pl. 159. 1920. TYPE: Colombia, Sierra del Libano, *Smith 2013* (MO, isotype).

Oligactis biattenuata (Rusby) Robinson & Brettell, Phytologia 28: 57. 1974.

Vine, the upper internodes densely arachnoid-villous, quickly glabrescent,

dark brown, striate. *Leaves* opposite, elliptic to lance-elliptic, denticulate with small, callose teeth, discolorous, the upper surface dark brown, glabrous or with a scattered arachnoid tomentum, felted-lanate beneath, white to tan, pinnately veined, lacking prominent lateral veins from the base; petioles ca. 1 cm long, subterete, felted-lanate. *Inflorescence* paniculate, terminal and axillary. *Heads* narrowly campanulate, ca. 8 mm high; involucre imbricate, 4–5-seriate; phyllaries indurate, the outer ovate, obtuse, ca. 1 mm long, ciliate, the inner becoming lanceolate, acuminate, ca. 5 mm long, mucronate; ray florets yellow, pistillate, fertile, the ligule 3–4 mm long, trifid, the style branches ca. 2.5 mm long, slender, acuminate; disc florets yellow, funnelform, 5–6 mm long, the corolla lobes 1–2 mm long, acute, the anthers exserted, the style branches ca. 1 mm long, slender, acuminate. *Achenes* turbinate, ca. 10-ribbed, ca. 1 mm long, puberulent; carpopodium distinct, annular, light tan; pappus of both ray and disc florets a single series of yellowish capillary bristles, persistent, ca. 5 mm long.

During the identification of various Panamanian Asteraceae, a collection of *Liabum biattenuatum* Rusby was discovered, a species previously known only from the Colombian Andes. This species is unique among the members of this genus in Panama in possessing leaves which are primarily pinnately veined and entirely lacking in prominent lateral veins arising from the base. This species most closely resembles *Liabum polyanthum* Klatt; however, it is readily distinguished from the latter by its smaller capitula and leaf venation.

PANAMA. CHIRIQUÍ: Cerro Horqueta, 7000 ft, *Blum & Dwyer 2618* (MO, SCZ).

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NAMES IN *AGALINIS* FOR SOME PLANTS THAT WERE CALLED *GERARDIA* AND *VIRGULARIA* (SCROPHULARIACEAE)

A New World group of plants with about 20 species in the eastern United States has, until recently, gone under the name *Gerardia*. The Montreal Code (Lanjouw et al., 1961) fixed the typification of *Gerardia* L. as applying to plants in the Acanthaceae and rejected the name against *Stenandrium* Nees (Acanthaceae). At the same time, *Agalinis* Raf. was conserved against *Chytra* Gaertner, making possible the substitution of the name *Agalinis* for the name *Gerardia* as formerly applied to plants in the Scrophulariaceae. This legislation was subject to considerable controversy (Thieret, 1956; St. John, 1957; Wherry, 1957; DeWolf, 1957; Thieret, 1958; Morton, 1959). All the required combinations have been made for the North American species and several important floras have made the substitution: Adams (1972); Correll & Johnston (1970); Radford et al.

(1964); and Long & Lakela (1971). Combinations have not yet been made for the species south of the United States. Because it is necessary to make a new combination for one species to appear in the *Flora of Panama*, it is timely to make the combinations for other species at the same time so the correct names will be available to workers on species growing outside of the United States. Except where noted, types have not been examined.

Agalinis angustifolia (Mart.) D'Arcy, comb. nov. *Gerardia angustifolia* Mart., Nov. Gen. Sp. Pl. 3: 12, *tab. 206*. 1829.

Agalinis brachyphylla (Cham. & Schlecht.) D'Arcy, comb. nov. *Gerardia brachyphylla* Cham. & Schlecht., Linnaea 3: 15. 1828.

Agalinis communis (Cham. & Schlecht.) D'Arcy, comb. nov. *Gerardia communis* Cham. & Schlecht., Linnaea 3: 12. 1828.

Agalinis domingensis (Spreng.) D'Arcy, comb. nov. *Gerardia domingensis* Spreng., Syst. Veg. 2: 807. 1825.

Agalinis fiebrigii (Diels) D'Arcy, comb. nov. *Gerardia fiebrigii* Diels, Bot. Jahrb. Syst. 37: 428. 1906.

Agalinis genistifolia (Cham. & Schlecht.) D'Arcy, comb. nov. *Gerardia genistaefolia* Cham. & Schlecht., Linnaea 3: 15. 1828.

Agalinis hispidula (Mart.) D'Arcy, comb. nov. *Gerardia hispidula* Mart., Nov. Gen. Sp. Pl. 3: 13. 1829. *Anisantherina hispidula* (Mart.) Pennell.

Agalinis humilis (Diels) D'Arcy, comb. nov. *Gerardia humilis* Diels, Bot. Jahrb. Syst. 37: 429. 1906.

Agalinis linarioides (Cham. & Schlecht.) D'Arcy, comb. nov. *Gerardia linarioides* Cham. & Schlecht., Linnaea 3: 12. 1828.

Agalinis megalantha (Diels) D'Arcy, comb. nov. *Gerardia megalantha* Diels, Bot. Jahrb. Syst. 37: 429. 1906.

Agalinis ramossisima (Benth.) D'Arcy, comb. nov. *Gerardia ramossisima* Benth. in DC., Prodr. 10: 515. 1846. TYPE: Brasil, *Gardner 566* (MO).

Agalinis reflexidens (Herzog) D'Arcy, comb. nov. *Gerardia reflexidens* Herzog, Meded. Rijks-Herb. 29: 37. 1916.

Agalinis rigida (Gill. ex Benth.) D'Arcy, comb. nov. *Gerardia rigida* Gill. ex Benth., Companion Bot. Mag. 1: 206. 1837.

Agalinis scarlatina (Herzog) D'Arcy, comb. nov. *Gerardia scarlatina* Herzog, Meded. Rijks-Herb. 29: 38. 1916.

Agalinis stenantha (Diels) D'Arcy, comb. nov. *Gerardia stenantha* Diels, Bot. Jahrb. Syst. 37: 429. 1906.

Agalinis tarijensis (R. E. Fries) D'Arcy, comb. nov. *Gerardia tarijensis* R. E. Fries, Ark. Bot. 6(11): 19. 1907.

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A NEW NAME FOR THE CHERRY TOMATO (*LYCOPERSICON*–SOLANACEAE)

Lycopersicon esculentum var. **leptophyllum** (Dun.) D'Arcy, comb. nov.

Lycopersicum cerasiforme Dun., Hist. Sol. 113. 1813.
L. humboldtii Dun., Hist. Sol. 112. 1813.
L. cerasiforme var. γ *leptophyllum* Dun. in DC., Prodr. 13(2): 26. 1852. LECTOTYPE: ?Nepal, *Wallich exsicc. 2611* (G-DC, not seen; microfiche, MO).
L. esculentum var. *cerasiforme* (Dun.) A. Gray, Syn. Fl., ed. 2. 2: 226. 1886.

This new combination is made in preparation for the treatment of the Solanaceae in the Flora of Dominica which is to be issued under the guidance of Dr. D. H. Nicolson, Smithsonian Institution. The plant under consideration is the Cherry Tomato, which is widely cultivated and is spontaneous in warm countries.

Variety *cerasiforme*, which is the currently used varietal name for the Cherry Tomato variety, is antedated at varietal rank by var. *leptophyllum* of 1852. Dunal used infraspecific names in his treatment of the Solanaceae for the de Candolle Prodromus, but he did not specify the intended rank. Accepted practice has considered these names as varieties. For example, Fernald (1900: 560) referred to *Solanum torvum* var. *ochraceo-ferrugineum* Dun. (Prodr. 260); Goodspeed (1954: 372) referred to Dunal's names under *Nicotiana tabacum* L. (Prodr. 556) as varieties; and Francey (1935: 126, 287, etc.) similarly referred to Dunal's names under species of *Cestrum* (Prodr. 601, 604, etc.) as varieties.

Schubert (1975) and Nicolson (1975) recently argued that the correct name for the tomato should be *Lycopersicon lycopersicum* (L.) Karst. rather than *L. esculentum* Mill., which has been traditional throughout much of this century. The issue revolves around how strictly tautonyms should be construed. Terrill (1977) argues that since the combination *Lycopersicon lycopersicum* was intended as a tautonym (and did take that form when first made) it should be so treated, and then *Lycopersicon esculentum* remains the correct name. Terrill

has proposed an adjustment to the Code which would clarify this issue and result in the continued use of *Lycopersicon esculentum*.

At issue is not only the logical purity of the Code versus pragmatic application, but the reputation of the taxonomic community among a significant part of the botanically interested public it seeks to serve. Thus I quote a recent letter from Charles M. Rick, a well-respected student of the genus *Lycopersicon*: "I have no useful comments to make in the matter of *L. esculentum* vs. *L. lycopersicum*. When taxonomists themselves are in such disagreement on this point, it is a pity that such a trivial historical quirk might result in great turmoil. Many tomato researchers are concerned that the change will cause great confusion and that the new name would be adopted with great irregularity (witness the continued usage of *Solanum lycopersicum*!). I can scarcely believe that the gain from a strict interpretation of the code would be worth all the confusion and agony that it will generate." Persistent use of the name *Vinca rosea* by growers in flagrant disregard of the correct name, *Catharanthus roseus*, is another example of taxonomists being unable to assert leadership over a skeptical public.

William T. Stearn once remarked to me that the greatest source of name changes is legislation: that is, changes in the Code which attempt to clarify one issue but which lead to changes in other names not under consideration at the time. Perhaps there is a limit as to how perfect the Code should be in terms of logical purity. Otherwise we are always burning the haystack to find the needle. It will be unpopular enough among the wide botanical community to substitute the name *leptophyllum* for the traditional var. *cerasiforme*; at least this is based on the long-standing principle of priority which can receive a sympathetic hearing when explained. Reinstatement of the name *L. lycopersicum* for *L. esculentum* after three-quarters of a century of use is entirely the result of legislative juggling, and the basic principles involved, if there are any, will be difficult to relate to others not directly involved in this series of Code manipulations.

In hopes that the taxonomic community will heed the practical and still logical arguments of Terrill and support his proposal or one much like it, the above combination is made under *L. esculentum* rather than under *L. lycopersicum*.

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A NEW *FREZIERA* (THEACEAE) FROM THE PANAMA/COLOMBIA BORDER

Freziera forerorum A. Gentry, sp. nov.—Fig. 1.

Species foliorum basibus plus magis inaequilateris a congeneribus diversa.

Slender tree 8 m tall. Branchlets strongly angled, with a line of trichomes below each node when young, soon glabrescent. Leaves sessile, oblanceolate, coriaceous, 8–18 cm long, 1.8–5.2 cm wide, acuminate at the apex, strikingly asymmetric at the base, the lamina on one side attenuate and ending 5–10 mm from the leaf base, lamina on other side cordate-auriculate, glabrous above, sparsely appressed puberulous below, the margin serrulate, the veins plane above, prominulous below. Flowers 1–3-fasciculate, axillary or borne below the leaves, the pedicels 3–4 mm long, glabrous, the 2 bracteoles glabrous except for sparsely ciliate margins; calyx lobes imbricate, suborbicular, glabrous, ca. 4 mm long; petals and stamens not seen; ovary glabrous, orbicular, attenuated into a style. Immature fruit small, subglobose, 3–4 mm in diameter, many seeded, the tiny seeds kidney-shaped, papillate.

Type: Panama. darién: Summit of Pico Tacarcuna, highest point of the Serrania del Darién, ca. 1900 m, 22 July 1976, *A. Gentry, H. León & L. Forero 16905* (MO, holotype; COL, PMA, and to be distributed, isotypes).

This plant keys to *F. angulosa* Tulasne in Kobuski's (1941) key, and is no doubt most closely related to that Bolivian species. It differs especially in the much narrower, strikingly more asymmetrical leaves with an accentuated basal lobe on one side. The pedicels are longer than in *F. angulosa*, while both bracteoles and pedicels are puberulous in that species.

This is a truly remarkable plant which may have the most asymmetric leaf base of any angiosperm. It comes from an equally remarkable place—the isolated summit of Pico Tacarcuna, almost exactly on the border between Colombia and Panama. The highest mountain between the Andes and western Panama, Cerro Tacarcuna has a unique relict vegetation. Almost one-fourth of the plant species collected in the oak forest above 1,400–1,500 m are undescribed. (See Gentry, 1977, for a description of the area.) *Freziera forerorum* is one of only five tree species which grow on the extreme summit of Cerro Tacarcuna. Interestingly, its congener *Freziera hieronymi* Kobuski (also new to Panama and to North America) is one of those four sympatric species. Unlike *F. hieronymi* and the other three species, *F. forerorum* appears to be limited to the summit of Pico Tacarcuna, a narrow ridge less than 50 m long. The vegetation of the flat summit ridge is an open montane thicket very different from the elfin forest of other exposed parts of the Tacarcuna massif and elsewhere in eastern Panama. *Freziera forerorum* appears to be restricted to this peculiar open montane thicket where extreme exposure to wind may be related to its stiff leaves with twig-clasping basal auricles. In view of its population of only a few individuals and the fact that all the trees (of all species) along the western edge of the summit ridge appear to be dying, this is no doubt an acutely threatened

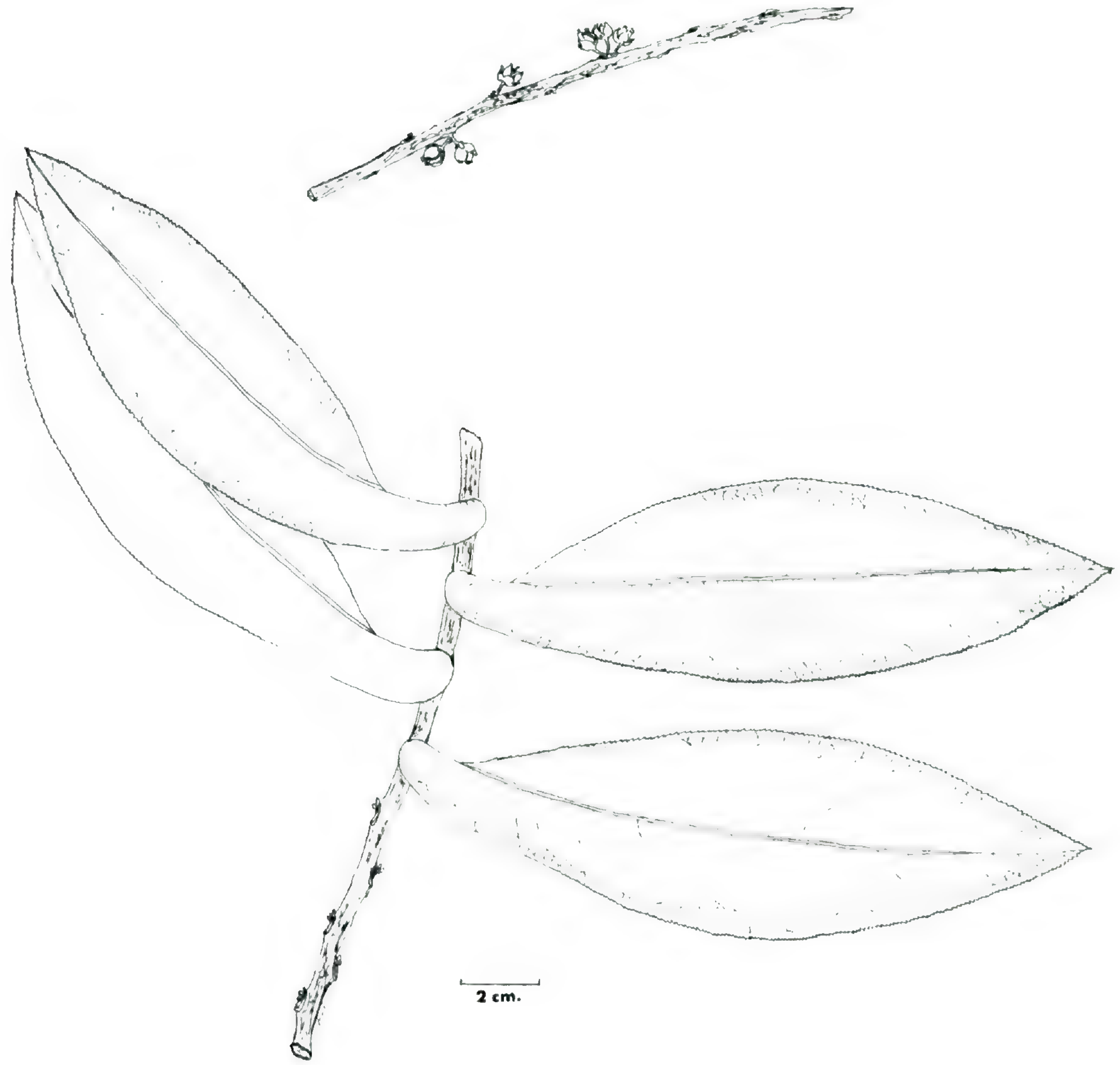

FIGURE 1. *Freziera forerorum* A. Gentry, *Gentry et al. 16905* (MO). Top: Fertile twig with old flowers and immature fruits. Bottom: Leafy twig.

species, one of the very few endangered species to whose demise man has not contributed.

I take pleasure in dedicating this species to two Colombian colleagues—Dr. Enrique Forero with whom I am conducting the floristic survey of the Chocó which led to its discovery and his student, Luis Forero, in whose company I found it.

This study was supported by NSF grant OIP 75-18202. I thank Dan Nicholson for discussion of the etymology and correct spelling of the specific epithet.

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THE IDENTITY OF *PAPAVER POLLAKII* KERNER

During the course of a biosystematic study of *Papaver* section *Oxytona* (Goldblatt, 1974) it seemed likely that the species *P. pollakii* described by Kerner von Marilaun in 1888 belonged to the section. The description was too brief and superficial to be certain, and the identity of *P. pollakii* could not be deduced from the published description. The type was believed to be housed at the Botanical Museum of the University of Vienna, but requests for the loan of authentic material in 1972 and 1973 proved fruitless and the specimens were thought to be part of a loan of *Papaver* to Humboldt University, Berlin. When a request to this institution to lend me possible type material of *P. pollakii* briefly to complete the study of types of species of sect. *Oxytona* elicited no response, I was obliged to publish the results of my study without being able to deal with *P. pollakii*. I have now received what appears to be authentic material comprising plants grown at Vienna, the progeny of seed collected by Dr. Pollak in northern Iran, in the vicinity of Ask. There are no annotations on any of the three specimens I have seen to indicate Kerner saw them, and no indication that these plants are actually types of *P. pollakii*. However, this material makes it clear that *P. pollakii* belongs to section *Oxytona* and is conspecific with *P. bracteatum*, one of the three species which I recognized in the section. The specimens are dated 1886 and 1887 and were grown at the Vienna Botanical Gardens. Almost certainly they are offspring of the original seed sent earlier to Vienna by Pollak. It seems reasonable to designate one of these specimens as lectotype, and I have selected the sheet bearing acquisition number 878. This is the only one of the three which has an open flower.

The determination is based on the following features. *Papaver pollakii* has quite dark red flowers with longitudinally blotched tepals and this pattern is consistent with the markings of *P. bracteatum*, the petals of which also dry a dark color. Specimens have four bracts, a low number for *P. bracteatum* though within the range of variation for this character, and the calyx bristles are broad based and appressed to the calyx surface exactly as in *P. bracteatum*. The other species of section *Oxytona* which has bracts is *P. pseudo-orientale* (Fedde) Medw., but this species seldom has more than two or three bracts, and it has more slender and usually erect calyx bristles, while its tepal markings are usually broad rather than long. Identification seems fairly certain and *P. pollakii* is thus to be treated as a synonym of *P. bracteatum*.

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CHROMOSOME NUMBER IN TWO CYTOLOGICALLY UNKNOWN NEW WORLD FAMILIES, TOVARIACEAE AND VIVIANIACEAE

In a recent survey of cytology in relation to angiosperm phylogeny, Raven (1975) drew attention to the remaining gaps in the chromosome records for families and taxonomically critical genera. A concerted effort has since been made by Raven and others to obtain cytological information for these taxa. This long-term project has yielded results for several groups and the two counts reported here represent the first records for two dicot families.

Tovaria was counted from pollen mother cells, material being fixed in the wild by A. Gentry. *Viviania* was grown from seed provided by O. Zöllner and counts were obtained from root tips. Root tips were treated as recently described by Goldblatt & Endress (1977).

VIVIANIACEAE

Viviania crenata Hook. $2n = 14$. Chile, Prov. Aconcagua, Resguardo Los Patos, 1200 m, *Zöllner 8316* (MO).

The family is traditionally included in Geraniaceae but is recognized by several recent phylogenists, including Hutchinson (1959), Takhtajan (1969), and Dahlgren (1975). As revised by Lefor (1975), it comprises four genera, all of southern South America. Vivianiaceae has been associated with several families apart from Geraniaceae, most notably Caryophyllaceae (Centrospermae) (Bortenschlager, 1967; Takhtajan, 1973) and Polemoniaceae (Lefor, 1971). Behnke & Mabry (1977) have shown quite conclusively on chemical and ultrastructural grounds that Vivianiaceae is not related to Centrospermae. A relationship with Polemoniaceae has received little support so that on balance, there seems every reason for treating Vivianiaceae in Geraniales, either as a separate family or in Geraniaceae.

Chromosome number of $n = 7$ in *Viviania crenata* accords with either placement, though not ruling out other treatments. Geraniaceae (sensu stricto) has high base numbers in all genera, with a range $x = 14$ through $x = 10$. Tropaeolaceae has $x = 14, 13, 12$, while lower base numbers are characteristic of Ledocarpaceae ($x = 9$), another segregate of Geraniaceae, and of Balsaminaceae ($x = 8$ and 7) and Limnanthaceae ($x = 5$). Vivianiaceae with $x = 7$ would seem to belong with this latter group, the low base number appearing discordant with the core genera of Geraniaceae itself.

TOVARIACEAE

Tovaria pendula R. & P. $n = 14$. Colombia, Antioquia Dept., Cañas Gordas, Medellin-Turbo, *Gentry & León 20205* (COL, MO).

Tovariaceae consists of two species in the single genus *Tovaria*, which ranges from northern South America to Mexico. The family is widely accepted as be-

longing to Capparales and, though generally accorded recognition, Thorne (1976) includes *Tovaria* in Capparaceae. Raven (1975) has suggested $x = 10$ or 11 as basic in Capparaceae, which has a range of numbers from $n = 17$, 16, 14, 12, 11, 10 and 8, while $x = 12$ (or possibly 14) seems basic in Cruciferae, in which a wide range of numbers occur. In the remaining families of the order, Resedaceae has $n = 10$, 6, 12, and 11 and Moringaceae $n = 14$ in the three species studied. *Tovaria* appears well placed in this alliance, and its base number of $x = 14$ accords well with Moringaceae and falls within the range recorded for Capparaceae, although $n = 14$ is unusual in this family, being reported only in two African genera, *Euadenia* and *Buchholzia*. The occurrence of $x = 14$ in another family of Capparales tends to support Raven's hypothesis of a tetraploid origin with $x = 14$ as basic for the order.

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I would like to thank Otto Zöllner for seed of *Viviania crenata* and Alwyn H. Gentry for the fixed buds of *Tovaria pendula*.

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ADDITIONS TO THE PANAMANIAN CONVOLVULACEAE

Since the publication of the Convolvulaceae in the *Flora of Panama* (Austin, 1975) several collections have been made of taxa new to the country. There has also been a name change.

1. **Ipomoea ramosissima** (Poir.) Choisy in DC., Prodr. 9: 377. 1845. Based on *Convolvulus ramosissimus* Poir.

Convolvulus ramosissimus Poir. in Lam., Encycl. Méth. Suppl. 3: 468. 1813. New name for *C. cymosus* Ruiz & Pavón.
C. cymosus Ruiz & Pavón, Fl. Peru 2: 9. *tab. 417. f.b.* 1799, non Desr., 1796. TYPE: Peru, Huanuco, *Ruiz & Pavón* (holotype presumably MA, not seen; F, isotype).

These plants are similar to *Ipomoea trifida* (H.B.K.) G. Don with which they have been confused previously. The flowers are smaller in *I. ramosissima* (13–24 mm long) than in *I. trifida* (30–40 mm long) and the sepals are shaped differently; obovate to elliptic-obovate in the former, ovate in the latter. While *I. ramosissima* is comparatively common in southern South America, it appears to be rare in Central America. It has been reported in Costa Rica under the name *I. quesadana* Standley (1940: 99) (*Austin-Smith 1609*, F, holotype), and in Guatemala as *I. perplexa* L. O. Williams (1970: 193) (Belize, Bartlett *12868*, MICH, holotype, not seen; F, isotype).

DARIÉN: *Duke 10217* (MO).

2. **Ipomoea indica** (Burm. f.) Merrill, Int. Rumph. Herb. Amb. 445. 1917, should replace the binomial *I. acuminata* (Vahl) Roem. & Schult. While Merrill transferred the epithet correctly, he did not typify the name. Because of doubt, various authors (e.g. van Ooststroom, 1953: 465; Verdcourt, 1963: 113) have considered the name suspect. F. R. Fosberg finally unraveled the cryptic comments in the Burman original and typified the epithet. *Ipomoea indica* is based on *Convolvulus indicus flore violaceo* Besler, Hort. Eyst. Aest. Ord. 13, *fig.* 2. 1613 (chosen lectotype by Fosberg, 1976).

3. **Maripa lewissi** D. Austin, sp. nov.

Frutex scandens, ramis lignosis teretibus glabris. Folia rigide coriacea, glabra, breviter obtuse acuminataque, 6–18 cm longa, 2–8 cm lata, petiolo 5–15 mm longo, nervo supra sulciformi subtus prominente. Paniculae terminales, basi foliatae, pyramidales, rachi glabra, cymis contractis. Sepala coriacea, interiora 4–5 mm, exteriora 5–6 mm longa, glabrata. Corolla purpurea, 10–12 mm longa. Fructus ellipsoideus, breviter apiculatus, 16–19 mm longus, abortu 1-locularis, 1-spermus, pericarpio coriaceo-lignoso tenui.

Lianas; stems terete, light to dark grey brown. Leaves with petioles 5–15 mm long; blades glabrous, ovate to oblong-elliptic or ovate-lanceolate, 6–18 cm long, 2–8 cm wide, the base rounded, the apex acuminate to obtuse-acuminate, coriaceous, the secondary veins 8–11 pairs. Inflorescences terminal, paniculate-thyrsiform; bracts triangular to triangular-subulate, 1–1.5 mm long, acute, persistent at anthesis and in fruit, glabrous. Flowers with the pedicels 3–4 mm long; sepals broadly ovate, the outer 5–6 mm long, the inner 4–5 mm long, coriaceous, glabrous or with scattered glandular indument; corolla cylindric-funnel form, lavender, 10–12 mm long, the lobes rounded; stamens included, the filaments 6 mm long, inserted 3 mm above the corolla base, the anthers narrowly ovate, basally sagittate, 2 mm long; ovary conic-oblong, 2 mm long, glabrous, the style 9 mm long. Fruits ellipsoid, 16–19 mm in diameter, rounded in cross-section, faintly striate, brown when dry, yellow when living, the calyx loosely appressed

against the fruit base; seeds 1, slightly flattened, oblong to ellipsoid, 12–14 mm long, 8–10 mm across, tan when dry.

TYPE: PANAMA. PANAMÁ, El Llano-Cartí road, 8 km N of Pan-American Highway at El Llano, 5 Mar. 1974, *Nee & Warmbrodt 10379* (MO, holotype; FAU, isotype).

The species is named for Walter H. Lewis who turned my attention to the tropical members of the Convolvulaceae in 1966. These lianas grow between 300–450 m in the Premontane Wet Forest and bloom in March. Fruiting specimens have been collected between May and December.

This is the only small-flowered (10–12 mm) member of the genus known in Central America. *Maripa panamensis* and *M. nicaraguensis*, which are the two species previously known from the area, have flowers 25–45 mm long. *Maripa lewissii* belongs to sect. *Maripa*, while the other two species in Central America are members of sect. *Mouroucoa* (Austin, 1973). All of the other members of sect. *Maripa* are known from east of the Andes Mountains.

Additional specimens seen: COLÓN: Santa Rita Ridge, 30 Dec. 1971, *Dwyer & Gentry 9341* (MO), 19 Sep. 1971, *Gentry 1858* (MO). PANAMÁ: El Llano-Cartí road, 8–11 km from Inter-American Highway, 14 Aug. 1975, *Mori 7740* (FAU, MO). 9.6 km from Inter-American Highway, 25 May 1975, *Mori & Kallunki 6375* (MO). 10–12 km from Inter-American Highway, 31 Oct. 1974, *Mori & Kallunki 2929* (FAU, MO). 7–12 km from Inter-American Highway, 18 July 1974, *Croat 25176* (MO). SAN BLAS: Inland from airport at Mandinga, 7 Oct. 1966, *Duke 8914* (MO).

KEY TO PANAMANIAN *Maripa*

a. Flowers 10–12 mm long; fruits 16–19 mm long ..... *M. lewisii* D. Austin
aa. Flowers 25–45 mm long; fruits 27–40 mm long.
  b. Leaves chartaceous to subcoriaceous, reticulate beneath, the veins prominent below; flowers densely sericeous outside; fruits smooth to slightly striate when dry ..... *M. nicaraguensis* Hemsley
  bb. Leaves thick-coriaceous, rugose beneath, the veins not prominent below; flowers tomentose outside; fruits strongly striate when dry ..... *M. panamensis* Hemsley

KEY TO *Maripa* sect. *Maripa*

a. External sepals appressed pubescent outside.
  b. Sepals light in color (whitish or yellowish) due to the dense cover of trichomes; fruits 20–30 mm long, the calyx tightly appressed ..... *M. scandens* Aublet
  bb. Sepals dark in color (purplish or with traces of white trichomes); fruits 30–35 mm long, the calyx loosely appressed ..... *M. paniculata* Barb.-Rodr.
aa. External sepals glabrous or with peltate scales outside.
  c. Internal sepals appressed dibrachiate-pubescent; all sepals appressed to base of fruits.
    d. Leaves with sunken oil glands above, glabrous below; ovary glabrous ..... *M. glabra* Choisy
  dd. Leaves without oil glands but with peltate scales or glabrous; ovary glabrous or pubescent.
    e. Sepals unequal, the outer 2 shorter; corolla indument balanced dibrachiate; fruits 27–30 mm long ..... *M. densiflora* Benth.
    ee. Sepals subequal; corolla indument balanced or unbalanced dibrachiate; fruits 25–35 mm long.
      f. Corolla indument balanced dibrachiate; fruits 30–35 mm long ..... *M. paniculata* Barb.-Rodr.
      ff. Corolla indument unbalanced dibrachiate; fruits 25 mm long ..... *M. janusiana* D. Austin

cc. Internal sepals glabrous outside or glandular; sepals loosely appressed or spreading in fruit.
g. Flowers 18–20 mm long; fruits 15–16 mm long, subglobose to widely ellipsoid, nonapiculate ..... *M. williamsii* v. Oost.
gg. Flowers 10–12 mm long; fruits 16–19 mm long, ellipsoid, shortly apiculate ..... *M. lewisii* D. Austin

Thanks are due Ron Liesner for pointing out the specimens on which *Maripa lewisii* is based and to Marshall Crosby for loaning the material.

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TRATTINICKIA ASPERA (BURSERACEAE) REPORTED NEW FOR SOUTH AMERICA

The *Flora of Panama* treatment for the Burseraceae by D. M. Porter (Ann. Missouri Bot. Gard. 57: 5–27. 1970) reported *Trattinickia aspera* (Standley) Swart to be endemic to Panama. The species has now been discovered in Colombia based on *Garcia-Barriga 3600* from the Commisaria del Putomayo, along the Mocoa Trail between Mocoa and Puerto Limón at an elevation of 500–600 m. The report of this species for Colombia is not at all surprising, but it is unusual that its first report for South America would be based on a collection made near the Ecuadorian border and on the edge of the Amazonian basin.

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A NAME CHANGE IN THE ANTILLEAN SOLANACEAE

Jaltomata antillana (Krug & Urban) D'Arcy, comb. nov.

Saracha antillana Krug & Urban, Notizbl. Königl. Bot. Gart. Berlin 1: 80. 1895. SYNTYPES: Jamaica, *Harris 5109*, 5522 (B, if extant, neither seen).

For notes on the separation of *Jaltomata* Schlecht. from *Saracha* R. & P. see Gentry, J. L. 1973. Restoration of the genus *Jaltomata* (Solanaceae). Phytologia 27: 286–288.

—*W. G. D'Arcy, Missouri Botanical Garden, 2345 Tower Grove Avenue, St. Louis, Missouri 63110.*

Second International Congress of Systematic and Evolutionary Biology

The Second International Congress of Systematic and Evolutionary Biology (ICSEB-II) will be held at the University of British Columbia, Vancouver, Canada, 17–24 July 1980.

The provisional list of symposia topics include:

1. Arctic Refugia and the Evolution of Arctic Biota
2. Origins and Evolution of the North Pacific Marine Biota
3. Evolution of Reproductive Strategies
4. Evolutionary Epigenetics
5. Evolution of Community Structure
6. Green Algae and Land Plant Origins
7. Macromolecular Mechanisms in Evolution
8. Allozymes and Evolution
9. Coevolution and Foraging Strategy
10. Evolution of Colonizing Species
11. Rare Species and the Maintenance of Gene Pools
12. Paleobiology of the Pacific Rim

Additional symposia may be included.

Sessions for contributed papers and for papers in specialized fields, taxonomic as well as methodological, will also be organized.

Those interested in receiving an information circular in the spring of 1979, should write to the following:

Dr. G. G. E. Scudder
Department of Zoology
The University of British Columbia
2075 Wesbrook Mall
Vancouver, B.C. V6T 1W5
Canada.

The previous two issues of the Annals of the Missouri Botanical Garden were published on the following dates: Vol. 64, No. 4, pp. 657–748 on 14 June 1978; Vol. 65, No. 1 on 12 October 1978.

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The ANNALS contains papers, primarily in systematic botany, contributed from the Missouri Botanical Garden. Papers originating outside the Garden will also be accepted. Authors should write the editor for information concerning arrangements for publishing in the ANNALS.

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Published four times a year by the Missouri Botanical Garden Press,
St. Louis, Missouri 63110.

For subscription information contact the Business Office of the Annals,
P.O. Box 368, 1041 New Hampshire, Lawrence, Kansas 66044.

Subscription price is $45 per volume U.S., Canada, and Mexico,
$50 all other countries. Four issues per volume.

Second class postage paid at Lawrence, Kansas 66044

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ANNALS
OF THE
MISSOURI BOTANICAL GARDEN

VOLUME 65 1978 NUMBER 3

FLORA OF PANAMA[1]

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part IX

FAMILY 175. GESNERIACEAE[2]*

LAURENCE E. SKOG[3]

Epiphytic or terrestrial *herbs*, *subshrubs*, *shrubs*, small *trees*, or *vines*, sometimes arising from tubers, or scaly rhizomes, or stolons; stems herbaceous, fleshy, suffrutescent to woody, erect, ascending, pendent, or scandent, simple or branched, usually pubescent at least toward the apex. *Leaves* opposite, rarely whorled or alternate, equal to strongly unequal, simple, entire to variously toothed, membranous, fleshy, or coriaceous; petioles usually present. *Inflorescences* axillary or terminal, the flowers solitary or in modified cymes or racemes, occasionally fasciculate. *Flowers* perfect; usually zygomorphic, rarely nearly actinomorphic; the floral tube composed of the combined adnate bases of the calyx, the corolla, and the stamens, short or long, in some genera surrounding and adnate to the inferior ovary; calyx of 4–5 lobes, free or connate at the base, equal or unequal, green or colored, entire or variously toothed; corolla variously

---

[1] Assisted by National Science Foundation Grant DEB 77-04300 (W. G. D'Arcy, principal investigator).

[2] Curators of several herbaria have made available their collections of Gesneriaceae for study in preparation of this treatment: A, BH, DUKE, F, FSU, GH, K, LE, MICH, MO, NA, NY, OS, PH, PMA, SCZ, US, USF, and the private herbarium of Clyde Reed, REED. Dr. Robert Dressler, Smithsonian Tropical Research Institute, kindly supplied fragments from collections of plants which had formed the basis of species described elsewhere. These fragments are designated as "Dressler coll." I thank all who helped in preparation of this treatment.

[3] Department of Botany, Smithsonian Institution, Washington, D.C. 20560.

* After this paper was in proof species of Panamanian Gesneriaceae were published by H. Wiehler in two papers: The Genera *Episcia*, *Alsobia*, *Nautilocalyx*, and *Paradrymonia* (Gesneriaceae). Selbeyana 5: 11–60. 1978; and Miscellaneous transfers and new species of Neotropical Gesneriaceae. Selbeyana 5: 61–93. 1978. Reference to these papers is made in footnotes bearing an asterisk (*).

0026–6493/78/0783–0998/20.85/0

colored, with a short or long tube of 5 connate petals, often oblique in the calyx, often gibbous to saccate at the base, cylindric, ventricose, or ampliate above, the limb of 4 or 5 equal or unequal lobes, sometimes bilabiate, erect or spreading to reflexed; stamens 4 (Panamá), with or without a staminode, or 5, included or exserted, usually didynamous, the filaments adnate to the base of the corolla tube, usually coiling or retracting after pollen shedding, the anthers variously shaped, coherent at first, dehiscing by pores or longitudinal slits; disc absent, or if present, annular or of 1–5 separate or connate nectariferous glands; ovary superior to inferior, 1-celled or rarely 2-celled, the 2 placentas parietal, the style usually elongating as the stamens retract, simple, the stigma usually bilobed or stomatomorphic (mouth-shaped). *Fruit* a berry or a dry or fleshy capsule, 2- or 4-valved; seeds numerous, more or less fusiform or oblong, very small, usually striate or otherwise variously marked.

The approximately 120 genera with an estimated 2,000 species of the Gesneriaceae are distributed throughout the world in tropical areas, rarely reaching into warm temperate regions. Many of the species are in cultivation as pot plants in temperate areas, prized for their flowers, particularly the African violet and the florist's gloxinia. From Panamá have come into cultivation many species of *Columnea* and other genera. Other than in horticulture the family has little economic value.

The Gesneriaceae are divided into 2 subfamilies, the Cyrtandroideae, found primarily in the Old World, and the Gesnerioideae, almost exclusively found naturally in the New World tropics. Morphologically, the 2 subfamilies are distinguished on characters of cotyledon development (Burtt, 1963).

The flowers are animal pollinated, either by bees, birds, particularly hummingbirds, butterflies, moths, and bats. The epiphytic habit is common in the Gesneriaceae allowing flying animals to visit for pollen and nectar, and for seed dispersal, although some species may have seeds dispersed by water or wind.

Twenty-seven genera and 147 species occur in Panamá, one of the most concentrated areas of distribution for the Gesneriaceae. Many of the genera and species occur also in Costa Rica and Colombia, or even farther north through Central America or south through the South American continent.

It was with considerable reluctance that this treatment was undertaken. Several botanists, including the late Conrad V. Morton, had begun the work in the past but, for one reason or another, it was not completed. Because of the urgency of the impending deadline for the completion of the Flora of Panama, the Missouri Botanical Garden wished to have, if possible, the treatment produced in a short time by someone familiar with the Gesneriaceae. Subsequently, the present author was asked to produce a treatment, as the most recent attempt by Hans Wiehler (Selby Botanical Gardens) could not be completed within the projected schedule. Only with the assurances of cooperation and support was the work begun.

It will be seen that some of the recently described species from Panamá are known only from the original descriptions as the types deposited at SEL were not available for study. In a few cases additional material attributable to those new taxa was seen and allowed the species to be better known.

Several new species had been discovered and annotated with herbarium names by Wiehler. It was hoped that these as yet unpublished names would be validated before the completion of this treatment of the Gesneriaceae. Rather than use unpublished names or take away credit for identifying the species as new, I have provided a description for the new but as yet unpublished species in the genera *Cremosperma*, *Drymonia*, and *Paradrymonia*, but have given them only a letter designation (e.g. *Cremosperma* species A). It is hoped that these species will soon be supplied with valid names.

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Wilson, C. L. 1974. Floral anatomy in Gesneriaceae II. Gesnerioideae. Bot. Gaz. (Crawfordsville) 135: 256–268.

a. Inflorescences terminal, rarely flowers in axils also, flowers in racemes; plants terrestrial from scaly rhizomes, or tubers, dying back to ground after flowering; ovary half to fully inferior, seldom nearly superior; fruit a dry capsule.
  b. Leaves in a rosette, silver or white spotted above. ..... 14. *Koellikeria*
  bb. Leaves cauline, not silver or white spotted above.
    c. Corollas red, not white or bluish; leaves sometimes whorled.
      d. Plants arising from tubers; ovary nearly superior; upper corolla lobes much longer than the other three, limb distinctly bilabiate ..... 26. *Sinningia*
      dd. Plants arising from scaly rhizomes; ovary ⅔ inferior; upper corolla lobes barely longer than the other, limb nearly regular ..... 15. *Kohleria*
    cc. Corollas not red, but white to cream, bluish or purplish; leaves not whorled.
      e. Tube of the corolla funnelform; disc glands 2–5 obvious; plants slender, seldom more than 25 cm tall ..... 9. *Diastema*
      ee. Tube of the corolla campanulate; disc glands lacking or very much reduced; plants often coarse, larger than 25 cm tall.
        f. Leaves acute to cordate, and not oblique at the base, often smooth above; floral tube grooved; corolla blue to lavender with a purple spot on the lower inside, rarely white ..... 13. *Gloxinia*
        ff. Leaves oblique at the base, often areolate above; floral tube not grooved; corolla usually white with a yellow area within, occasionally with bluish limb or all blue ..... 16. *Monopyle*

aa. Inflorescences axillary, not terminal, flowers in cymes or modified cymes, sometimes congested or solitary; plants usually lacking modified underground stems, or with scaly rhizomes, or rarely tubers, terrestrial or epiphytic; ovary inferior to superior; fruit a berry or a dry or fleshy capsule.
  g. Plants producing stolons, terrestrial low herbs; fruit a fleshy capsule; flowers solitary, rarely more, corollas white to blue or red ..... 11. *Episcia*
  gg. Plants lacking stolons, terrestrial or epiphytic, of various habit; fruit a berry or a dry or fleshy capsule; flowers of various numbers, corollas variously colored.
    h. Corollas subactinomorphic, usually white, rarely bluish or pinkish; plants low terrestrial herbs.
      i. Plants arising from scaly rhizomes; stem obvious; ovary half-inferior ..... 23. *Phinaea*
      ii. Plants lacking underground stems, acaulescent with the leaves closely appressed to the ground, or with a very short stem; ovary superior ..... 18. *Napeanthus*

hh. Corollas zygomorphic, tube usually elongate, corollas usually red, but occasionally white, purplish, greenish, orange or pink; plants terrestrial or epiphytic herbs, subshrubs, shrubs, or small trees.
j. Ovary half to fully inferior.
k. Low terrestrial herbs; plants from scaly rhizomes.
k'. Disc annular, entire ..... 1. *Achimenes*
k". Disc of 5 separate glands, rarely 2 or 3 connate ..... 9. *Diastema*
kk. Large shrubs, epiphytes or small trees; plants lacking underground stems (or rarely occurring in *Capanea*).
l. Corollas campanulate, pale green to greenish-white, with purple spots; plants usually epiphytic and scandent, seldom terrestrial ..... 4. *Capanea*
ll. Corollas slender, ventricose or gradually broader from the base, red; plants terrestrial, erect.
m. Calyx tube elongate above the ovary; corollas 5.5–7.0 cm long; small trees ..... 27. *Solenophora*
mm. Calyx tube very short above the ovary; corollas 4 cm or less long; shrubs ..... 17. *Moussonia*
jj. Ovary nearly to fully superior.
n. Leaves truly alternate, terrestrial plants ..... 24. *Reldia*
nn. Leaves opposite, sometimes strongly unequal and the smaller leaf in a pair bract-like or caducous; terrestrial or epiphytic plants.
o. Plants from tubers, terrestrial; stems succulent; leaves opposite and equal; calyx lobes red or green, all connate nearly to apex ..... 5. *Chrysothemis*
oo. Plants lacking tubers, rarely with any underground stem, terrestrial or epiphytic; stems occasionally succulent, more commonly herbaceous to woody; leaves opposite, but often unequal; calyx lobes red or green, but not all connate to the apex.
p. Plants terrestrial or at the base of trees; disc annular, somewhat lobed, or unlobed, or rarely reduced to a single posterior gland (*Gasteranthus dressleri*), but then the plants very short with leaves appressed to ground; inflorescences bractless.
q. Stems very short, to 15 cm tall; corolla narrowly funnelform, less than 1.3 cm long; leaves less than 6.6 cm long, membranous; fruit a capsule ..... 8. *Cremosperma*
qq. Stems usually much taller than 15 cm; corollas tubular, ventricose or subcampanulate, usually more than 1.3 cm long; leaves usually much more than 7 cm long; membranous to coriaceous; fruit a berry or capsule.
r. Fruit a berry; disc annular to semiannular; corollas usually tubular, rarely subcampanulate, spur not prominent ..... 3. *Besleria*
rr. Fruit a capsule; disc semiannular, with a posterior thickening, or reduced to a single gland; corollas usually subcampanulate, ampliate, and with a prominent spur ..... 12. *Gasteranthus*
pp. Plants epiphytic or terrestrial; disc usually reduced to a single posterior gland or 2–5 separate glands; inflorescences rarely lacking bracts, but bracts sometimes caducous.
s. Anthers dehiscing by pores; corollas spurred; usually epiphytic, but sometimes terrestrial in large-leaved taxa in *Drymonia*; fruit a berry or fleshy capsule.

t. Leaves always glabrous, 6 cm long or less; plants all epiphytic, often on ant nests; corollas waxy, with pink or red areas; bracts small, green ..... 6. *Codonanthe*

tt. Leaves pubescent or glabrous, usually much longer than 6 cm long; plants epiphytic or terrestrial; corollas variously colored from white to purple; bracts often large and colored ..... 10. *Drymonia*

ss. Anthers dehiscing by longitudinal slits; corollas spurred or not; epiphytic or terrestrial; fruit a berry or a dry or fleshy capsule.

u. Fruit a berry; plants epiphytic, rarely terrestrial.

v. Flowers congested in the leaf axils; plants epiphytic; stems erect or ascending; leaves nearly equal in a pair; corollas white suffused with pink or red, or red on the upper side.

w. Fruit apically pointed; corolla tubular, inflated, white and red, or pink flushed ..... 21. *Oerstedina*

ww. Fruit globose or compressed; corolla broadly funnelform, somewhat bilabiate, lower side and lower 3 lobes white, upper 2 lobes reddish ..... 25. *Rufodorsia*

vv. Flowers not congested in the leaf axils; plants mainly epiphytic, seldom terrestrial; stems often pendent, but sometimes erect or ascending; leaves equal to very unequal in a pair; corolla usually red or yellow with variously colored lines or spots (white with pink or brown spots in *Neomortonia*).

x. Inflorescences lacking bracts, 1-flowered; corolla broadly funnelform, the lower lobe nearly erect, the others patent, margin laciniate; plants pendent; leaves 1.8 cm long or less, blades nearly equal in a pair; disc reduced to a single dorsal gland ..... 20. *Neomortonia*

xx. Inflorescences bearing bracts, although sometimes caducous, 1–few flowered; corolla variously shaped, but lower lobe erect if the other lobes erect, usually reflexed, lobes rarely patent, margin entire to erose; plants erect to pendent, leaves usually much longer than 1.8 cm, blades in a pair equal to strongly unequal; disc of 1–5 glands ..... 7. *Columnea*

uu. Fruit a dry or fleshy capsule; plants usually terrestrial, but rarely epiphytic, except in *Paradrymonia*.

y. Corolla white to yellow with purple lines or spots, rarely reddish or all purple; red or yellow, tube densely puberulent, hirsute or white sericeous,

lobes very short; leaves elliptic, oblong, ovate or obovate ..... 2. *Alloplectus*

yy. Corolla white to yellow with purple lines or spots, rarely reddish or all purple; tube sparsely pubescent or villous; lobes elongate; leaves usually elongate lanceolate.

z. Stem often very short, much exceeded by the elongate lanceolate leaves; flowers densely congested in the leaf axils (except long-pedunculate in *Paradrymonia pedunculata*), corollas white or yellow to purplish, with red or purple lines; plants usually epiphytic ..... 22. *Paradrymonia*

zz. Stem usually longer than the leaves; flowers not congested, corollas white or cream, occasionally with pink lines; plants terrestrial ..... 19. *Nautilocalyx*

1. ACHIMENES

Achimenes Pers., Syn. Pl. 2: 164. 1806, nom. cons. against *Achimenes* P. Browne. TYPE: *A. coccinea* (Scop.) Pers. = *A. erecta* (Lam.) H. P. Fuchs.

Trevirana Willd., Enum. Pl. Hort. Berol. 637. 1809. TYPE: *T. coccinea* (Scop.) Willd. = *Achimenes erecta* (Lam.) H. P. Fuchs.

Locheria Regel, Flora 31: 251. 1848. LECTOTYPE: *L. hirsuta* (Lindl.) Regel = *Achimenes skinneri* Lindl.

Guthnickia Regel, Flora 32: 179. 1849. TYPE: *G. mimuliflora* Regel = *Achimenes antirrhina* (DC.) Morton.

Dicyrta Regel, Flora 32: 181. 1849. TYPE: *D. warszewicziana* Regel = *Achimenes warszewiczziana* (Regel) H. E. Moore.

Eumolpe Decne. in Jacq. & Herincq, Man. Gén. Pl. 2: 575. 1849. TYPE: *E. fimbriata* Decne. = *Achimenes glabrata* (Zucc.) Fritsch.

Scheeria Seem., Bot. Mag. 79: *tab. 4743.* 1853. TYPE: *S. mexicana* Seem. = *Achimenes mexicana* (Seem.) Benth. & Hook. f. ex Fritsch.

Plectopoma Hanst., Linnaea 26: 201. 1854. TYPE: *P. fimbriatum* Hanst. = *Achimenes glabrata* (Zucc.) Fritsch.

Perennial, terrestrial *herbs* from underground scaly rhizomes; stems erect to decumbent, seldom elongate, usually pubescent to pilose, unbranched. *Leaves* opposite or 3 in a whorl, nearly equal to very unequal in a pair, membranous, variously toothed; petioles short. *Inflorescences* axillary, of single flowers or of 2 or more in a short cyme. *Flowers* often showy; floral tube turbinate; calyx of 5 free, entire lobes; corolla erect or oblique in the calyx, either tubular with a flat spreading limb, or obliquely funnelform, often swollen or spurred on the upper side at the base, the 5-lobed limb nearly regular to 2-lipped, lobes broad, spreading or nearly erect, entire to fringed, the lower 3 lobes usually larger; stamens 4, included, didynamous, the filaments adnate to the base of the corolla tube, slender, the anthers oblong or quadrate, united apically; disc annular, cup-like, entire; ovary ½ to completely inferior, 1-celled with 2 parietal placentas, the style curved, the stigma bilobed, stomatomorphic or cupulate. *Fruit* a bivalved capsule, the apex conic.

About 25 species of *Achimenes* are known, mainly from Central America, but also in Jamaica and South America.

Achimenes has been in cultivation for 200 years, introduced to England from Jamaica in 1778 and is widely grown today in Europe and the United States. Plants are easily propagated and grown for their showy flowers. Most of the known species are available commercially along with many cultivars.

At least three species occur in Panamá. *Achimenes erecta* (Lam.) H. P. Fuchs is reported by many sources as occurring in Panamá, but no authentic specimens of the species have been seen. *Achimenes erecta* differs from the red-flowered *A. pedunculata* by having a corolla erect in the calyx, from the blue-flowered *A. longiflora* by having a reddish corolla only up to 2.5 cm long, and from the white-flowered *A. candida* by color and the nearly cylindric corolla.

The origin of the generic name *Achimenes* is unknown. The first user of the name, Patrick Browne, gave no explanation. Later authors have attempted, without success, to discover its derivation.

Literature:

Arnold, P. 1969. The Gesneriad Register: *Achimenes*. American Gloxinia and Gesneriad Society. 40 pp.

Morton, C. V. 1962. The Species of *Achimenes*, Section *Dicyrta*. Baileya 10: 147–154.

a. Corolla white with red spots; stems glabrous; stigma stomatomorphic ..... 1. *A. candida*
aa. Corolla red, orange, or blue to purple; stems villous or pilose; stigma bilobed.
b. Corolla erect in the calyx, blue to purple, not spurred ..... 2. *A. longiflora*
bb. Corolla oblique in the calyx, red and spotted, short spurred at base ..... 3. *A. pedunculata*

1. **Achimenes candida** Lindl., J. Hort. Soc. London 3: 317. 1848. TYPE: Guatemala, *Skinner* (not seen).

Trevirana candida (Lindl.) Decne., ex van Houtte, Fl. Serres Jard. Eur. 4: *tab. 420.* 1848.
Diastema gracilis Regel, Flora 32: 180. 1849. TYPE: Guatemala, *Warscewicz* (not seen).
Dicyrta candida (Lindl.) Hanst., Linnaea 27: 715. 1856.
Kohleria saxicola T. S. Brandeg., Univ. Calif. Publ. Bot. 6: 66. 1914. TYPE: Finca Mexiquito, Chiapas, México, *Purpus* 6853 (MO, US, isotypes).
Achimenes saxicola (T. S. Brandeg.) Morton, Bull. Misc. Inform. 1936: 14. 1936.

Herbs; stems slender, erect or ascending, 6–50 cm tall, 1–2 mm in diam., green or reddish, nearly glabrous. *Leaves* very unequal, the larger more than 4 times the size of the smaller, membranous, ovate to elliptic, often falcate, the larger 3.4–10.2 cm long, 0.9–3.7 cm wide, the smaller 0.5–4.8 cm long, 0.2–2.0 cm wide, the apex acuminate, the base oblique, acute to cuneate, the margin coarsely serrate, the upper surface light green, sparsely villous, the lower surface lighter green to whitish, villous especially on the veins; petioles 0.3–1.1 cm long, pilose on upper surface. *Inflorescences* cymose, few flowered; peduncles short or obsolete; bracts minute; pedicels ca. 1 cm long; floral tube 1–2 mm long, sparsely villous; calyx lobes spreading, linear lanceolate, 2–4 mm long; corolla 1.5–2.5 cm long, the tube erect in calyx, swollen at the base, not spurred, curved toward the mouth, flattened top and bottom, white outside with reddish spots, inside yellowish with red spots or purple veins, nearly glabrous, the limb ca.

12–18 mm wide, the lobes white, undulate, nearly entire; filaments glabrous; disc lobed; ovary apex pilose, the style white, nearly glabrous, the stigma stomatomorphic. *Capsule* narrowly obconic, ca. 5 mm long, the base surrounded by the floral tube, the apex conic and curved, surrounded by the persistent calyx lobes, sparsely villous, green to brown; seeds fusiform, striate, twisted, ca. 0.25 mm long, dark reddish brown. *Chromosomes* $n = 11$ (Lee & Grear, 1963).

This species is found in México, Guatemala, Costa Rica, and in the province of Chiriquí in Panamá where it is rare. Where it has been located near Boquete, it grows in gravel. Because fruit and seeds were not seen on Panamanian material, part of the above description was taken from *Reko 3481c* (US) from México.

CHIRIQUÍ: 1 mi SW of Boquete, 4000 ft, *Allen 4724* (MO, US). Boquete (Salta), 4000 ft, *Davidson 844* (US); 1200–1500 m, *Woodson & Schery 764* (MO, US).

2. **Achimenes longiflora** DC. Prodr. 7: 536. 1839. TYPE: "Peru, *Pavon*" [México, Sessé & Mociño] (G-DC, holotype; US, photo).—FIG. 1.

Achimenes pauciflora Oerst., Cent. Gesn. 17. 1858. TYPE: Mt. Aguacate, Costa Rica, *Oersted* (C, type; US, photo).

A. *longiflora* var. *margaritae* Klotzsch ex Hanst., Linnaea 28: 708. 1858. TYPE: Volcán Chiriquí, Panamá, *Warscewicz* (not seen).

Gesneria longiflora Sessé & Mociño, Pl. Nov. Hisp., ed. 1, 97. 1889. TYPE: "Peru, *Pavon*" [México, *Sessé & Mociño*] (G-DC, holotype; US, photo).

Herb; stems erect or ascending, 10–40 cm tall, 2–3 mm in diam., green or reddish, villous; branches few. *Leaves* opposite or 3 at a node, nearly equal in a pair, lanceolate to ovate, 1.9–5.9 cm long, 0.8–2.7 cm wide, the apex acute, the base cuneate to acute, the margin serrate, green above and villous, below pale green or more usually reddish between the veins; petioles short. *Inflorescences* of single axillary flowers; pedicels ca. 0.5 cm long, densely pilose. *Flowers* showy; floral tube 2–5 mm long, densely pilose; calyx lobes linear lanceolate, 7–12 mm long, glabrescent, long ciliate; corolla blue or lavender (Panamá), erect in the calyx, lacking a spur, the tube narrow, 3.5–6.5 cm long, ca. 0.5 cm wide at the base, spotted or lined, glabrous, the limb oblique, broad, flat, 3.9–6.5 cm wide, nearly regular, the lobes entire; stamens included, nearly equalling the corolla tube, the filaments adnate to the base of the corolla tube, glabrous; style puberulous, the stigma 2-lobed. *Fruits* and seeds not seen on Panamá material. *Chromosomes* $n = 11$ (Eberle, 1956).

Achimenes longiflora is the most common and widespread of species of *Achimenes* in Central America, known from México to Panamá. It is also considered one of the most attractive because of its large flowers. Numerous varieties have been named from wild material because of its variable form. Outside Panamá the flowers vary from white to purple, with yellow or red markings. The species is also common in cultivation and many cultivars are or were available.

In Panamá plants may be found in wet areas in forests, on shaded banks near streams, and on rock outcrops. It occurs in the provinces of Chiriquí, Coclé, Los Santos, and Panamá.

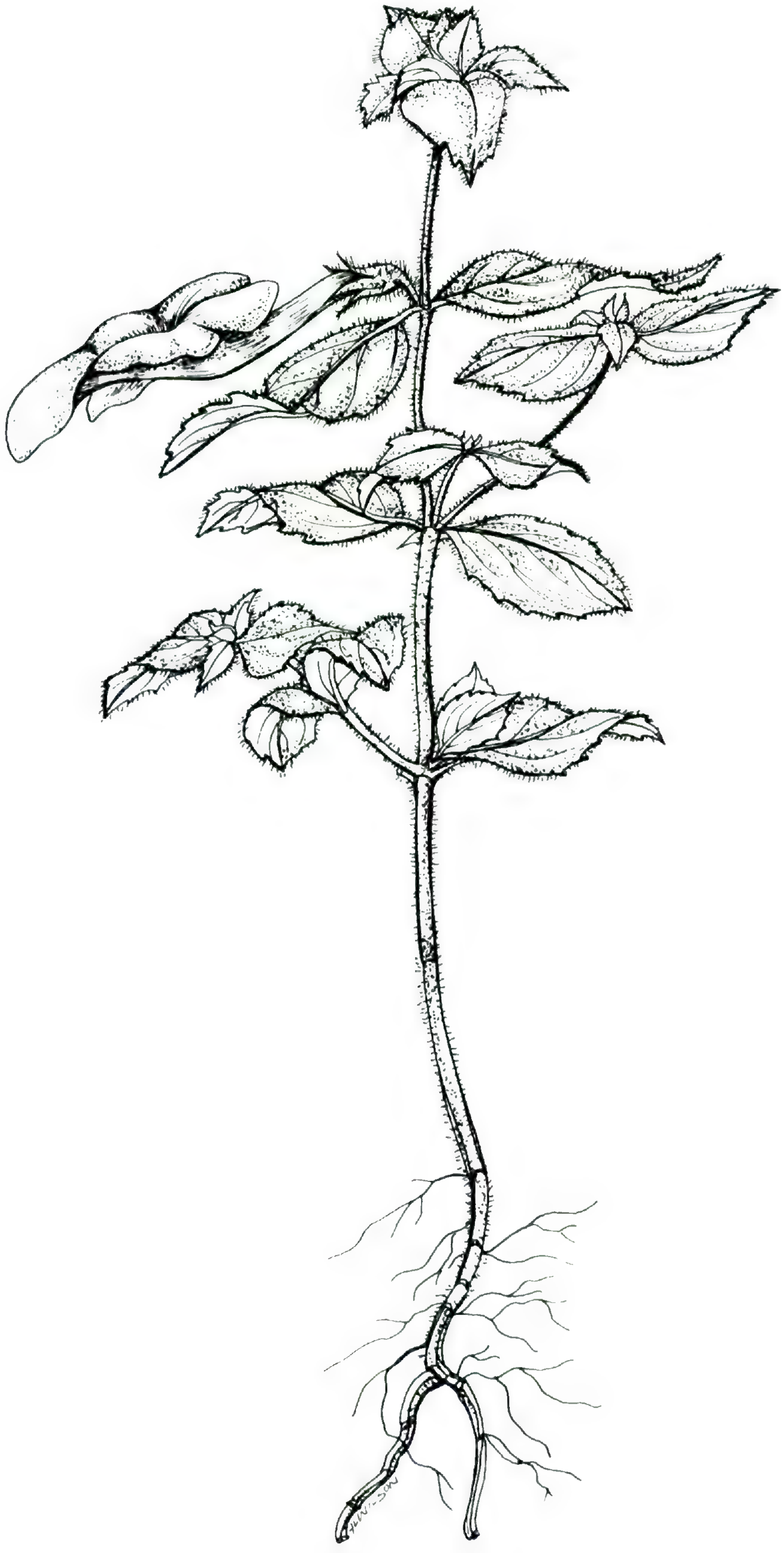

FIGURE 1. *Achimenes longiflora* DC. Habit (×9/10). [After *Luteyn 1573* (MO).]

CHIRIQUÍ: 5 mi S of Boquete, 3000 ft, *Allen 4698* (MO). Cerro Colorado, ca. 50 km N of San Félix, near mining camp, 750–800 m, *Dressler 5130* (PMA). Boquete, Llanos Francia, 3300 ft, *Stern et al. 1202* (MO). Boquete, 1200–1500 m, *Woodson & Schery 737* (MO). COCLÉ: El Valle, 800–1000 m, *Allen 109* (MO), *744* (MO, NY). Hills S of El Valle de Antón, 650 m, *Allen 2746* (US). El Valle, *Dwyer 1846* (MO). Km 21 on road to El Valle, *Gentry 5614* (MO, SCZ). Western slope and summit of Cerro Valle Chiquito, 700–800 m, *Seibert 496* (K, MO, NY, US). Between Las Margaritas and El Valle, *Woodson et al. 1731* (MO, NA, NY, US). LOS SANTOS: Río Tonosí ca. 9 mi N of Tonosí where the bridge crosses towards Guaniquito, *Luteyn & Foster 1383* (DUKE). PANAMÁ: Río Teta E of San Carlos where it passes under Highway 1, *Luteyn 1573* (F, DUKE, MICH, MO). Río Mar, *Tyson et al. 2297* (SCZ).

3. **Achimenes pedunculata** Benth., Pl. Hartw. 78. 1841. TYPE: Santa María, Guatemala, *Hartweg 546* (K, holotype; P, isotype, US, photo).

Locheria pedunculata (Benth.) Regel, Flora 31: 252. 1848.

Herbs; stems erect, 0.4–1.0 m tall, ca. 5 mm in diam., green or reddish to purple especially near the nodes, pilose to glabrate, internodes elongate, to ca. 20 cm long; scaly propagules occasional in leaf axils. *Leaves* opposite, nearly equal in a pair, ovate or broadly elliptic, 5.5–13.2 cm long, 3.6–9.8 cm wide, cuspidate acuminate at the apex, the base rounded to cordate, often oblique, the margin sharply serrate, dark green and sparsely villous to scabrous above, below light green, puberulent; petioles elongate, 0.5–6.5 cm long, reddish on the upper side, pilose. *Inflorescences* in the upper leaf axils, cymose or racemose, longer than the subtending leaves; peduncles when present up to 10.5 cm long, sometimes lacking, green to red, pilose; bracts linear, pilose, often bearing scaly propagules in axils; pedicels 1–8 cm long, puberulent. *Flowers* 1 to several, showy; floral tube 3 mm long, scabrous or puberulous; calyx lobes narrowly triangular to oblong or ovate, 3–6 mm long, green, scabrous puberulous, entire, not ciliate; corolla red, scarlet, orange red, or orange or yellow on the underside, red spotted, the tube short-spurred, oblique in the calyx, gradually ampliate above from the narrow base, 2.5–3.5 cm long, ca. 0.5 cm wide at the base, to ca. 1 cm above, sparsely glandular-pubescent outside, inside yellow, red spotted, the limb regular, the lobes spreading, rounded, entire, red orange or yellow with red lines; stamens included, the filaments curved, adnate to the base of the corolla, pilose; style pilose, the stigma bilobed. *Fruits* and seeds not seen in Panamá material. *Chromosomes* $2n = 34$ (Fussell, 1958).

This species is rare in Panamá, known from a single collection from Chiriquí province, but otherwise it has been collected from southern México to Colombia.

Achimenes pedunculata is distinctive because of its long-pedunculate inflorescences and tall habit.

CHIRIQUÍ: Las Lagunas, 12 km SE of Volcán, 1300 m, *Dressler 5155* (MO, PMA, US).

2. ALLOPLECTUS

Alloplectus Mart., Nov. Gen. 3: 53. 1829. TYPE: *A. sparsiflorus* Mart., conserved name and type (see below).

Crantzia Scop., Intr. 173. 1777. TYPE: *Besleria cristata* L. = *Alloplectus cristatus* (L.) Mart.

Lophia Desv., in Hamilton, Prodr. Pl. Indiae Occid. 47. 1825, illegitimate name for *Crantzia* Scop. TYPE: *L. phoenicia* Desv. ex Hamilton, illegitimate name for *Besleria cristata* L. = *Alloplectus cristatus* (L.) Mart.

Lophalix Rafin., Sylva Tell. 70. 1838. TYPE: *L. bicolor* Rafin., illegitimate name for *Besleria cristata* L. = *Alloplectus cristatus* (L.) Mart.
Heintzia Karst., Auswahl. Gewachse Venezuela 34. 1848. TYPE: *H. tigrina* Karst. = *Alloplectus tigrinus* (Karst.) Hanst.
Glossoloma Hanst., Linnaea 26: 191, 208, 209. 1854. TYPE: *G. tetragona* Hanst. = *Alloplectus tetragonus* (Hanst.) Hanst.
Prionoplectus Oerst., Cent. Gesn. 45. 1858. LECTOTYPE: *Prionoplectus cristatus* (L.) Oerst. = *Alloplectus cristatus* (L.) Mart.

Shrubs or coarse *herbs*, terrestrial or epiphytic; roots fibrous; stems erect or clambering, quadrangular. *Leaves* opposite, usually equal in a pair, often long petiolate, elliptic to ovate or oblanceolate, entire to serrate. *Flowers* 1 to few in fascicles, axillary, bracteate, the peduncles not evident; calyx usually colored or green, the 5 lobes nearly free, often broad, entire to strongly serrate, pubescent to pilose; corolla tubular, yellow or red, oblique in the calyx, constricted or not in the throat, or laterally compressed, gibbous at the base with a spur, often ventricose below the mouth, the 5 lobes of the limb usually small; stamens 4, not exserted, the filaments adnate to the base of the corolla tube, the anthers often transversely oblong, coherent or becoming free, dihiscing by longitudinal slits; disc gland large, sometimes 2-lobed; ovary superior, the apex pilose, the style included. *Fruit* a fleshy bivalved capsule surrounded by the persistent calyx; seeds numerous, striate.

Alloplectus is a genus of about 60 species distributed mainly in northern South America. The plants usually occur in rain or cloud forests as terrestrials or epiphytes, and appear quite commonly at forest margins.

A few species are cultivated, but are not particularly ornamental.

When Oersted described *Prionoplectus* in 1858, he included 3 species, and did not single out one as a type species. Of the two combinations Oersted made in the genus, *Prionoplectus cristatus* (L.) Oerst. is here selected as the lectotype for the genus.

In the original publication of *Alloplectus* Martius included several species. One of these, *A. sparsiflorus*, was chosen to lectotypify the genus when *Alloplectus* was included in the list of conserved names in the International Code of Botanical Nomenclature. More recently Wiehler (1972) included *Alloplectus sparsiflorus* in the genus *Nematanthus* Schrader as a synonym of *N. hirtellus* (Schott) Wiehler on the basis of leaf characters and cytology. Thus it might appear that *Alloplectus* and *Nematanthus* are synonymous which they are not. *Nematanthus*, which was described in 1821, is a distinct genus occurring in southeastern Brasil and is not known in Panamá. When a new lectotypification is made for *Alloplectus* the distinctiveness of the two genera will be clarified.

The generic name is derived from the Greek words for "other" and "fold," and refers to the often recurved calyx lobe margins.

Literature:

Morley, B. D. 1974. A Revision of the Caribbean species in the genera *Columnea* L. and *Alloplectus* Mart. (Gesneriaceae). Proc. Roy. Irish Acad. 74(B)24: 411–438.
Morton, C. V. 1944. Taxonomic studies of tropical American plants. Contr. U.S. Natl. Herb. 29: 1–19.

Stearn, W. T. 1969. The Jamaican species of *Columnea* and *Alloplectus*. Bull. Brit. Mus. Nat. Hist. (Bot.) 4: 181–236.

Wiehler, H. 1971 [1972]. Name changes for some American Gesneriaceae in cultivation. Baileya 18: 133–137.

———. 1973. One hundred transfers from *Alloplectus* and *Columnea* (Gesneriaceae). Phytologia 27: 309–329.

a. Leaves entire, glabrous above; calyx lobes crenulate to entire, 3–7 mm long, 2–3 mm wide; corolla 1.2–2.1 cm long ..... 5. *A. pycnosuzygius*

aa. Leaves denticulate, serrate or serrulate, pilose, pilosulus, or strigillose above; calyx lobes strongly serrate, dentate, or fimbriate, at least toward apex, 0.8–3.5 cm long, 5 mm or more broad, usually longer and much wider.

b. Stem epidermis peeling off in scales: leaves strongly veined below; corolla constricted at limb, 1.5–2.3 cm long ..... 2. *A. ichthyoderma*

bb. Stem epidermis not peeling off in scales; leaves strongly veined or not; if corolla constricted at limb, then leaves not strongly veined below.

c. Corolla constricted at limb, to 3.0 cm long; internodes red spotted.

d. Calyx lobes serrulate, 8–10 mm long; corollas to 1.2 cm long, puberulent; ovary puberulent ..... 1. *A. ambonensis*

dd. Calyx lobes fimbriate, to 2 cm long; corollas to 2.9 cm long, densely pilose; ovary densely pilose ..... 3. *A. medusaeus*

cc. Corolla ampliate toward limb, 3.5–5.0 cm long; internodes not red spotted.

e. Calyx lobes broadly orbicular ovate, more than 10 mm wide; leaf bases cuneate to narrowly acute ..... 6. *A. tetragonus*

ee. Calyx lobes oblong, 10 mm wide or less; leaf blades acute, bases rounded, or truncate ..... 4. *A. panamensis*

1. **Alloplectus ambonensis** L. Skog.[4] TYPE: Panamá, *Folsom et al. 4774* (US, holotype; MO, US, isotypes).

Terrestrial *subshrubs*; stems quadrangular, erect to 1.7 m tall, 1 cm or more thick, above puberulent near the apex, below red spotted and glabrescent, somewhat scaly or appearing so from the red spots, the internodes often elongated to 12 cm long; unbranched. *Leaves* nearly equal in a pair; blades broadly elliptic, occasionally falcate, 12–20 cm long, 6–12 cm wide, membranous, the apex acute to acuminate, the base acute to cuneate, crenulate or denticulate, above dark green, glabrous, below green to purplish, strigillose, the veins prominent, the petioles 5–8 cm long, 1–2 mm thick, red spotted, strigillose. *Inflorescences* axillary, cymose, several flowers in a group; peduncles commonly short or nearly lacking, 1–3 mm long; bracts lanceolate, ca. 8 mm long, reddish, strigillose; pedicels 1–2 cm long, elongating in fruit, red spotted, strigillose. *Flowers* with the floral tube costate, strigillose; calyx tube ca. 5 mm long, the lobes ovate, 8–10 mm long, 8 mm wide, the tube appearing cordate at the base, the apex acute, variously toothed, outside yellow green at the base to orange red at the apex and the margin, or rarely all green, strigillose, inside sparsely pubescent; corolla yellow or cream colored, the tube oblique in the calyx, funnelform to urceolate, the base ca. 6 mm in diam., ampliate and ventricose on lower side at middle to 1.2 cm, then constricted at the throat to 6 mm, outside puberulent, the inside glabrous, the limb oblique, the lobes nearly equal, repent, ca. 1.5 mm long, 4–5 mm wide; stamens included, the filaments curved, adnate

[4] *Alloplectus ambonensis* L. Skog, sp. nov. *Alloplectus ichthyoderma* Hanst. affinis, differt caulibus maculatis epidermide squamas simulantibus, fructibus albis glabris et corollis puberulis.

to the base of the corolla tube for 2–5 mm, free part 5–8 mm long, white, glabrous, the anthers oblong, 3–4 mm long, 2–3 mm wide, the locules parallel; disc reduced to a bilobed posterior gland; ovary ovoid, 3 mm long, puberulent, the style curved above, 1 cm long, white, the stigma stomatomorphic, papillate. *Fruit* broadly globose, 5 mm long, 5–6 mm in diam., white, glabrous, weakly dehiscent in 2 valves; seeds fusiform, 0.5–1.0 mm long, obliquely striate, dark reddish brown, each attached to a white funicle.

This species of *Alloplectus* is found in nearly the same habitats as *A. ichthyoderma* in the Province of Chiriquí, and it greatly resembles that species in inflorescence structure, leaf form, habit, and in the red stem spots which mimic the scaly pattern in *A. ichthyoderma*. The species described here differs in the glabrous white fruit and in having a puberulent rather than a sericeous corolla. Another species to which this species is similar in habit is *Paradrymonia metamorphophylla* (J. D. Smith) Wiehl. However, *P. metamorphophylla* differs in having a much more congested inflorescence, laciniate calyx lobes, sericeous upper leaf surfaces, and often very unequal leaf pairs.

BOCAS DEL TORO: Róbalo Trail, N slopes of Cerro Horqueta, 6000–7000 ft, *Allen 4976* (MO). CHIRIQUÍ: Cerro Colorado, ca. 50 km N of San Félix, 1400 m, *Dressler 5095* (PMA). Trocha 3 de Noviembre, between Alto de Guayabo and Paso de la Zorra, 1400–1600 m, *Dressler 5470* (PMA). Road along ridge [Cerro Colorado] last stream before rising to antenna, 1650 m, *Folsom et al. 4774* (MO, US). Cerro Colorado, 50 km N of San Félix on the continental divide, cloud forest, 1200–1500 m, *Mori & Dressler 7818* (MO, US). Chiriquí Trail, between Pinola and Quebrada Hondo toward summit, *Kirkbride & Duke 885* (MO, MO, REED).

2. **Alloplectus ichthyoderma** Hanst., Linnaea 34: 372. 1865. TYPE: Costa Rica, *Wendland 833* (not seen).

Columnea ichthyoderma (Hanst.) Kuntze, Rev. Gen. 2: 472. 1891.
Crantzia ichthyoderma (Hanst.) Fritsch, Nat. Pflanzenfam. 4(3b): 168. 1894.
Alloplectus ruacophilus J. D. Smith, Bot. Gaz. (Crawfordsville) 54: 238. 1912. TYPE: Forests of Volcán Barba, Prov. Heredia, Costa Rica, *Tonduz 1997* (US, holotype).

Terrestrial or epiphytic coarse colonial *herbs* or *shrubs*; stems erect to 1.5 m tall, to 1 cm across, usually unbranched, hirsute; internodes elongate; epidermis peeling off in scales. *Leaves* well spaced, nearly equal, usually present from the stem apex down to 3 or 4 nodes below the apex; blades elliptic to oblong to obovate, 7–20 cm long, 3–8 cm wide, the apex acute to acuminate, the base cuneate to acute, occasionally oblique, denticulate to serrate, membranous, green and appressed pilose above with prominent impressed veins, much lighter green or rarely reddish and strigillose below, with prominent veins; petioles slender to coarse, sulcate above, 1.0–5.5 cm long, 2–3 mm wide, green, appressed hirsute, with reddish glandlike structures at the juncture of the petiole and the stem. *Inflorescences* axillary, cymose, of 1 to several flowers in a fascicle; peduncles short, the bracts 2, lanceolate to ovate, ca. 1 cm long, 0.5 cm wide, reddish, subentire; pedicels 0.5–1.5 cm long, green to reddish, appressed pilose. *Flowers* with the floral tube densely white pilose, the calyx somewhat oblique, 5-lobed, the lobes shortly connate at the base, lanceolate to ovate, to 1.8 cm long, red, green, or green with red margins, the apex obtuse to acuminate, serrate to lacineate, white sericeous especially toward the midvein; corolla horizontal in the calyx, tubular,

15–23 mm long, yellow to orange or reddish outside, white sericeous, yellow inside, gibbous at the base, ventricose on the upper side toward the apex, but constricted at the throat, the limb oblique, 5-lobed, ca. 8 mm wide, nearly regular, the lobes orbicular, ca. 2 mm across; stamens 4, included, filaments glabrous; ovary apex tomentose, the style glabrous, the stigma stomatomorphic. *Fruit* surrounded by the persistent calyx, globose to ovoid, white and fleshy. *Chromosomes* $n = 9$ (Davidse, 1970, based on material from Costa Rica).

Alloplectus ichthyoderma is known from Costa Rica south to northern South America. In Panamá the species is found in the Province of Chiriquí. Its habitat is usually in damp areas or near streams in rain forests at high elevations.

This species most closely resembles *Alloplectus ambonensis* L. Skog, but differs in having smaller calyces, white fruits and larger, thinner leaves. Another close relative, *Alloplectus medusaeus*, differs in having fimbriate calyx lobes.

CHIRIQUÍ: Cerro Punta, 2000–2500 m, *Allen 3528* (MO, NY, US). Bajo Mono-Róbalo Trail, W slopes of Cerro Horqueta, 5000–7000 ft, *Allen 4826* (MO, US). N Cerro Copete, an eastern spur of Chiriquí Volcano, 8000–8500 ft, *Allen 4873* (MO, US). Summit and SW face of Cerro Copete, 9000 ft, *Allen 4906* (MO, US). Las Nubes, 5.5 km NW of Río Chiriquí Viejo, W of Cerro Punta, 2200 m, *Busey 664* (DUKE, MO, NY, US), *684* (MO). 2.2 km SW of Cerro Punta on road above I.D.A.A.N. water tank, along ridge trail SW of Quebrada Iglesia, 2100–2250 m, *Croat 26299* (MO). Above Cerro Punta, 7600 ft, *D'Arcy 5349* (MO). Top of ridge above Bajo Chorro, *D'Arcy 11064* (MO, US). Bajo Chorro, Boquete District, 7500 ft, *Davidson 207* (MO, US). Volcán de Chiriquí, Boquete District, 10500 ft, *Davidson 1024* (MO, US). Road to Bajo Grande, *Folsom 4014* (MO, US). Slopes of Cerro Punta, 2000 m, *Gentry 5864* (MO). Along Boquete Trail, Cerro Respinga, E of town of Cerro Punta, 2000–2500 m, *Gentry 5956* (MO). Las Nubes, 2.7 mi NW of Río Chiriquí Viejo W of Cerro Punta, 2200 m, *Liesner 297* (US). Las Nubes, 5 km NW of Cerro Punta, 6000–6500 ft, *Mori & Bolton 7256* (MO). Trail in remnant oak forest, Cerro Punta, 2.5 km SE of town, *Mori & Kallunki 5645* (MO, US). Bajo Grande, 1–3 km E of town of Cerro Punta, 2000–2200 m, *Nee 10014* (MO, US). Cuesta de Las Palmas, southern slope of Cerro de la Horqueta, 1700–2100 m, *Pittier s.n.* (US). Cerro Punta, 6800 ft, *Ridgeway & Solis 2411* (MO, US). Trail to Alto Respinga above town of Cerro Punta, 2500 m, *Skog et al. 4005* (MO, US), *4026* (E, MO, P, PMA, US). 6 mi above Cerro Punta on the Boquete Trail, 7500 ft, *Tyson 7166* (PMA). Montane rain forest, W slopes of Cerro Respinga, NE of Cerro Punta village, 2000–2250 m, *Webster & Breckon 16531* (MO). Trail from Bajo Grande along the Quebrado Grande to the top of Paso de Respingo on the trail to Boquete, 2100–2400 m, *Wilbur et al. 15145* (DUKE, F, MICH, MO). 2.5 km NE of Cerro Punta 7200 ft, *Wilbur et al. 17158* (DUKE). Recently opened ravine W of Las Nubes, 5 km NW of Cerro Punta and towards Cerro Picacho, 2000–2100 m, *Wilbur & Luteyn 19394* (DUKE). Trail between Cerro Punta and the Quebrado Bajo Grande, 2000–2100 m, *Wilbur et al. 11921* (DUKE, MICH, MICH, MO, NY). Trail through the Paseo de Respinga on way to Boquete, 7500 ft, *Wilbur & Teeri 13176* (DUKE). Trail between Las Mirandas and Las Nubes and a small valley running NW of the mountain of Cerro Punta 3 mi from village of Cerro Punta, *Wilbur & Teeri 13273* (DUKE). E of Guadeloupe along the Río Chiriquí Viejo 2 km NE of Cerro Punta, ridge of Cerro Respinga, 7000 ft, *Wilbur et al. 13089* (DUKE, F, MO). NW side of Cerro Punta beyond Las Nubes, 7500 ft, *Wilbur et al. 13201* (DUKE, MICH, MO). Casita Alta to Cerro Copete, 2300–3300 m, *Woodson & Schery 359* (MO, US).

3. **Alloplectus medusaeus** L. Skog.[5] TYPE: Panamá, *D'Arcy & D'Arcy* 6398 (US, holotype; MO, isotype).

Terrestrial or epiphytic *herbs* or *subshrubs*; stems erect, to 1.5 m tall, 1 cm in diam. or more below, the apex densely strigillose, below sparsely strigillose to glabrescent, the internodes red spotted, more dense toward the apex and sparse

[5] *Alloplectus medusaeus* L. Skog, sp. nov. *Alloplectus ichthoderma* Hanst. affinis, differt epidermide caulis squamatis destituta et calycis fimbriatis.

below. *Leaves* nearly equal in a pair, elongate elliptic or narrowly obovate, 20–28 cm long, 6–11 cm wide, membranous, the apex acuminate, the base cuneate, sharply serrulate, above green, sparsely strigillose, below pink to purple, strigillose especially along the prominent veins; petioles elongate, slender, 3.5–10.5 cm long, reddish, strigillose. *Inflorescences* in the upper axils, fasciculate cymose; 1–6 flowers per axil; peduncles lacking; bracts caducous, elliptic, ca. 5 mm long, reddish, strigillose, nearly entire; pedicels 0.7–3.0 cm long, strigillose. *Flowers* with the floral tube short, densely pilose; calyx lobes lanceolate to ovate, 1.0–2.5 cm long, ca. 1 cm wide at the widest point, the margin somewhat recurved, fimbriate, the teeth to 5 mm long, green to yellow or reddish, outside strigillose to pilose, inside pubescent to strigose, pilose toward base; corolla pale yellow to pinkish, oblique in the calyx, the tube gibbous on the upper side at the base, 2.5–3.0 cm long, ca. 6 mm in diam. at the middle, broadening to ca. 8 mm, then narrower at the limb, 6–7 mm, the outside glabrous at the base, from the middle and above densely pilose, the inside glandular, the lobes of the limb erect, ovate, 2 mm long and wide, entire; stamens included, the filaments adnate to the base of the corolla tube ca. 5 mm, curved above, reddish, glabrous, the anthers broad, ca. 1.5 mm long, 2 mm wide, back reddish, connective broad, reddish; disc reduced to a broad dorsal gland; ovary subglobose, densely pilose to sericeous, the style 15 mm long, glabrous, the stigma narrowly stomatomorphic. *Capsule* immature, globose or ovoid, densely pilose; seeds not seen.

This species resembles both *Alloplectus ichthyoderma* Hanst. and *Drymonia macrophylla* (Hanst.) Moore. From the first, which inhabits nearby sites, this species differs most obviously in lacking the scaly epidermis and in having a fimbriate calyx. From the second this species lacks the typical anthers of *Drymonia*, has a smaller, densely pilose corolla, and occurs at much higher elevations. Collections of the species described here have been made in the provinces of Bocas del Toro, Chiriquí, Coclé, and Darién, and in Costa Rica.

BOCAS DEL TORO: Róbalo Trail, N slopes of Cerro Horqueta, 6000–7000 ft, *Allen 4993* (MO, US). CHIRIQUÍ: Slope of La Popa above Boquete, 5400 ft, *D'Arcy & D'Arcy 6398* (MO, US). Road along ridge, Cerro Colorado, last stream before rising to antenna, 1650 m, *Folsom et al. 4776* (MO, US). Cerro Colorado, 50 km N of San Félix on the continental divide, 1200–1500 m, *Mori & Dressler 7813* (MO). COCLÉ: Above El Valle, *Folsom 3119* (MO). DARIÉN: Valley between Cerro Pirre and next most southerly peak, *Folsom 4496* (US).

4. **Alloplectus panamensis** Morton, Ann. Missouri Bot. Gard. 29: 36. 1942. TYPE: Hills N of El Valle de Antón, Prov. Coclé, Panamá, *Allen 2189* (US, holotype; MO, US, isotypes).—FIG. 2.

Terrestrial or rarely epiphytic robust, suffrutescent *herbs* or *shrubs*; stems erect, to 2.5 m tall, to 1.5 cm in diam., woody, quadrangular, unbranched, densely yellow hirsute on the younger stems, glabrescent below, the internodes elongate, to 10 cm long. *Leaves* at the stem apices, equal in a pair, mostly ovate, 10.5–23.0 cm long, 6.2–15.0 cm wide, acuminate, the base acute to rounded or truncate, serrate or serrulate, chartaceous, above dark green to dull reddish, pilose, below lighter green or coppery to maroon with prominent green veins, densely pilose; petioles sulcate, elongated, to 15 cm long, to 5 mm wide, hirsute. *Inflorescences* axillary, 1–4 flowered; peduncles not evident; bracts leaflike, ovate, 0.1–1.5 cm

FIGURE 2. *Alloplectus panamensis* Morton. Habit (×½). [After *Porter et al. 4356A* (MO).]

long, acuminate, red, pilose; pedicels 2–3 cm long, reddish, wooly hirsute. *Flowers* orange red with the floral tube conical, densely pilose with reddish hairs; calyx red, the lobes erect, nearly equal, oblong, 1.5–2.0 cm long, 0.5–1.0 cm wide, acute, glandular serrate, sparsely to densely yellow or reddish pilose on both sides especially on the outside at the base; corolla salmon to orange or red, oblique in the calyx, the tube 3.5–5.0 cm long, the base gibbous, ca. 4 mm wide above the gibbosity, gradually broader to 1.1 cm wide at mouth, not ventricose, the outside hirsute, the inside glandular, the limb oblique, ca. 1.5 cm across, the lobes recurved, nearly equal, orbiculate, each ca. 3–4 mm long, and 5 mm wide, entire; stamens adnate to the base of the corolla tube for ca. 5 mm, included, the filaments ca. 3 cm long, yellow, glabrous, the anthers coherent, oblong to orbicular, 1–2 mm long, yellow; disc gland one, thick, glabrous, emarginate; ovary pilose, style ca. 3 cm long, yellow, glabrous, the stigma bilobed, papillate. *Fruit* surrounded by the persistent calyx, ovoid, splitting to expose the white placenta; seeds brown, 0.5–1.0 mm long, oblong, striate.

Alloplectus panamensis individuals are coarse plants occupying openings or margins of forests from 100 to 1,400 m in the provinces of Bocas del Toro, Coclé, Darién, Panamá, and Veraguas in Panamá. The species is also known from Colombia (Chocó) and from Costa Rica.

BOCAS DEL TORO: Between Quebrada Lugrón and Cerro Bonyic, near Río Terebe, 300–900 ft, *Kirkbride & Duke 645* (MO, NY). Fish Creek Mountains, Chiriquí Lagoon, *Wedel 2308* (MO, US, US). COCLÉ: Hills N of El Valle de Antón, 1000 m, *Allen 2166* (US), *2189* (MO, US, US). El Valle de Antón, north hills, *Allen 3555* (MO, US). Trail to Cerro Pilón WEPCOR weather site, ca. 1 km from top, 900 m, *Correa 56* (DUKE, FSU, SCZ). La Mesa above El Valle de Antón, 800 m, *Croat 14387A, 25391* (both MO). Road past Furlong's Finca, due N of Cerro Pilón, 880 m, *Croat 37552* (MO). Hills N of El Valle de Antón, *Dressler 2956* (US). Slopes of Cerro Pilón near El Valle, 700–900 m, *Duke 12065* (MO, REED). El Valle, 800–1000 m, *Duke 13171* (MO, OS). Foothills of Cerro Pilón, near El Valle, 900 m, *Duke & Correa 14699* (MO). Cerro Gaital Carocoral, 2700–3200 ft, *Dwyer & Correa 8845* (F, MO). La Mesa, El Valle, 2500 ft, *Dwyer & Duke 8274* (MO); *Dwyer & Nee 11922* (MO, PMA), *11925* (MO). El Copé, El Petroso, Atlantic slope of Alto Calvario, *Folsom & Lantz 1885* (MO, US). La Mesa N of El Valle, 1000 m, *Gentry 6859* (MO, PMA). El Valle side area of WEPCOR, Cerro Pilón, *Kirkbride 1081* (MO). Cerro Pilón, 2700 ft, *Lallathin 5068, 6004* (both MO). Mountains N of El Valle de Antón, 2500–3000 ft, *Lewis et al. 1730* (MO). Cerro Pilón, 900–1173 m, *Liesner 772* (MO). La Mesa, 4 km N of El Valle, 875 m, *Nee & Hale 9653* (MO). Foot of Cerro Pilón above El Valle de Antón, 2000 ft, *Porter et al. 4356A* (MO), *4485* (MO, SCZ). La Mesa above El Valle, 800 m, *Skog & Butcher 4127* (MO, US). El Petroso, at Rivera's saw mill, 7 km beyond El Copé, 800 m, *Skog et al. 4196* (MO, US). Road from village of El Valle to La Mesa, *Spellman et al. 554* (MO). La Mesa above El Valle de Antón, 1000 m, *Weaver & Foster 1636* (DUKE). La Mesa, 3 km N of El Valle de Antón, 850 m, *Wilbur et al. 15621* (DUKE, DUKE, MO). Inside the crater of El Valle de Antón on La Mesa below the north rim, 1000 m, *Wilbur et al. 11151* (DUKE, MO). DARIÉN: Cerro Pirre, near triangulation marker, 1400 m, *Folsom 4338* (MO). PANAMÁ: Campo Tres, 5 km NE of Altos de Pacora, *Busey 814* (US). Summit of Cerro Jefe and forests beyond summit, *Hayden 1007* (MO). VERAGUAS: Beyond Tres Brazos River along steep descent 11 km beyond Santa Fé, 650 m, *Croat 25651* (MO). Valley of Río Dos Bocas along road between Escuela Agricola Alto Piedra and Calovébora, 15.6 km NW of Santa Fé, 450–550 m, *Croat 27660* (MO). Continental Divide, third branch of Río Santa María to drop-off to lowlands, 12–15 km NW of Santa Fé, 650–750 m, *Dressler 4826* (PMA). 5 mi W of Santa Fé on road past Escuela Agricola Alto Piedra on Pacific side of divide, 800–1200 m, *Liesner 872* (US). 11 km from Escuela Agricola Alto de Piedra, in forest along Río Dos Bocas, *Mori & Kallunki 3090* (MO, US). 16 km NW of Santa Fé on road to Calovébora, 300–500 m, *Mori & Kallunki 6110* (MO, US). Road to agriculture school, 3–4 km by road W of Santa Fé, 2500 ft, *Nee 11310* (MO).

5. **Alloplectus pycnosuzygius** (J. D. Smith) Morton, Fieldiana, Bot. 28: 522. 1953.

Besleria pycnosuzygia J. D. Smith, Bot. Gaz. (Crawfordsville) 52: 53. 1911. TYPE: In forests at La Palma, Prov. San José, Costa Rica, *Tonduz 12545* (US, holotype; US, isotypes).

Epiphytic *shrub*; stems arching, to 2.5 m tall, quadrangular, strigillose at the apex, glabrescent below, unbranched, the internodes slender, 1.5–7.6 cm long, the nodes thicker. *Leaves* unequal, the larger about 3 times the size of the smaller, elliptic to obovate or oblanceolate, 5.4–19.8 cm long, 1.6–7.2 cm wide, the apex acuminate, the base acute to truncate, entire, subcoriaceous, green and glabrous above, below pale green, sparsely pubescent on the prominent veins; petioles to 2 cm long, puberulent. *Inflorescences* axillary, of 1–6 flowers; peduncles not evident; bracts small, oblong; pedicels 6–14 mm long, ca. 1 mm in diam., reddish, appressed puberulent. *Flowers* with the floral tube turbinate, verrucose, red and pubescent; sepals 5, briefly connate at the base, lanceolate to oblong, 3–7 mm long, 2–3 mm wide at the base, the apex acute, crenulate to

entire, red, the outside puberulous, the inside white pilose; corolla appearing pink from white pilose or sericeous hairs covering the red surface, tubular, oblique in the calyx and about 3 times as long as the calyx, 1.2–2.1 cm long, ca. 2 mm in diam. at the base above the spur, gradually wider to 5–6 mm wide at the mouth of the curved tube, the limb regular, the lobes minute, ca. 1 mm long, rotund, nearly equal; stamens included, the filaments adnate to the base of the corolla tube for about 4 mm, the anthers coherent, transversely elliptic, ca. 1 mm long, 2 mm wide, locules not confluent; disc thick, glabrous; ovary ovoid, ca. 3 mm long, villous; style ca. 1.5 cm long, sparsely pubescent. *Fruits* ovoid, ca. 7 mm long, reddish, villous, surrounded by the persistent calyx.

Alloplectus pycnosuzygius is a rarely-collected species from Costa Rica and Panamá. Where it is known in Panamá plants occur as epiphytes on trees in rain forest above 1,900 m in the provinces of Bocas del Toro and Chiriquí.

BOCAS DEL TORO: Róbalo Trail, northern slopes of Cerro Horqueta, 6000–7000 ft, *Allen 4996* (F, MO, NY, US, US). CHIRIQUÍ: Bajo Chorro, 1900 m, *Woodson & Schery 683* (MO).

6. **Alloplectus tetragonus** (Hanst.) Hanst., Linnaea 34: 368. 1865.

Glossoloma tetragona Hanst., Linnaea 26: 209. 1854. TYPE: Turrialba, Costa Rica, *Oersted* (not seen).
Columnea tetragona (Hanst.) Kuntze, Rev. Gen. 2: 472. 1891.
Crantzia tetragona (Hanst.) Fritsch, Nat. Pflanzenfam. 4(3b): 168. 1894.
Alloplectus ichthyoderma Hanst. var. *hirsutulus* Morton, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1145. 1938. TYPE: Atirro, Prov. Cartago, Costa Rica, *Smith 6715* (US, holotype).
A. simulatus Morton, Ann. Missouri Bot. Gard. 29: 37. 1942. TYPE: Panamá, *Woodson & Schery 537* (US, holotype; MO, isotype).
A. fraternus Morton, Proc. Biol. Soc. Washington 69: 193. 1956. TYPE: Panamá, *Allen 1000* (MO, holotype; US, isotype).

Terrestrial or rarely epiphytic *herbs* or *shrubs*; stems erect, 0.5–2.0 m tall, quadrangular, succulent, becoming woody, to ca. 1 cm in diam., green to brown, hirsute with yellowish hairs above, glabrescent below; internodes short or long; unbranched. *Leaves* nearly equal in a pair, narrowly elliptic to oblong, 14–25 cm long, 4–11 cm wide, acuminate, the base cuneate or acute, serrate or serrulate, membranous, above green and sparsely pilose especially on the veins, pale green and strigose or hisute beneath; petioles sulcate, elongate, 5–8 cm long, ca. 2 mm wide, sparsely to densely pilose. *Inflorescences* axillary, erect, of 1–4 flowers; peduncles not evident; bracts ovate, ca. 9 mm long, ca. 4 mm wide, red or green, acuminate, denticulate, hirsute; pedicels 2–5 cm long, red or green, pilose. *Flowers* showy; floral tube short, densely pilose; calyx erect, slightly oblique, the base truncate, the lobes connate briefly at base, each orbicular or ovate with a broad base, to 2.7 cm long, to 2 cm broad, all green, all red, orange or green with red margins, the margin apex acute to acuminate, strongly serrate from the base, hirsute on both sides, the midvein especially pilose, the inside hirsute to glabrous; corolla red or appearing orange or yellow from dense yellow hairs, inside yellow, tubular, oblique, slightly curved, laterally compressed, 3.5–5.0 cm long, the base gibbous, ca. 4 mm in diam. above the gibbosity, ampliate toward the limb, not contracted in the throat, the mouth somewhat ventricose, oblique, outside pilose, inside glabrous; limb subregular, ca. 1.7 cm

broad, the lobes free, nearly equal, ca. 3 mm long and 3–6 mm broad, entire; stamens included, filaments adnate to the base of the corolla tube, glabrous, the anthers transversely oblong, 1–2 mm long, 2–3 mm wide, white, coherent; disc of a single large, entire gland, glabrous; ovary apex pilose, the style glabrous, the stigma stomatomorphic. *Fruit* pendent when ripe, ovoid, green; seeds numerous, fusiform, dark brown, 0.5–1 mm long, striate. *Chromosomes* $n = 9$ (Wiehler, 1972).

This species is widespread through Central America and northwestern South America. In Panamá it can be found in the provinces of Bocas del Toro, Chiriquí, Panamá and Veraguas from 450 to 2,000 m elevation.

One population from Veraguas province is inconsistent in having green sepals and narrower leaves than others. Since these characters are usually quite variable over the full range, the population is not here separated taxonomically.

BOCAS DEL TORO: Róbalo Trail, N slopes of Cerro Horqueta, 6000–7000 ft, *Allen 4981* (MO, US). Between Quebrada Gutierrez and E ridge of La Zorra, headwaters of Río Mali, *Kirkbride & Duke 717* (MO). CHIRIQUÍ: Llanos on slopes of Volcán de Chiriquí and along Río Chiriquí Viejo, 1200 m, *Allen 1000* (MO, US, US). Palo Santo, 3 mi N of Volcán, *Croat 13572* (MO, MO, NY). 1 mi E of Cañas Gordas near Costa Rican border on road to Volcán, *Croat 22314* (MO, NA). Cerro Colorado Copper Mine Development, 28 mi above San Félix, 9–10 mi above turnoff to Escopeta, 1200–1500 m, *Croat 33207* (MO). 2.5 km from Questa Piedra along Río Monte Road, *Folsom 3985* (MO, US). Cerro Colorado, 11.2 km along ridgeroad from main road to Escopeta, 1700 m, *Folsom 4885* (MO, US). Bajo Mona and Quebrada Chiquero, 1500 m, *Woodson & Schery 537* (MO, US). PANAMÁ: Cerro Campana, 1000 m, *Allen 2412* (US). Near summit of Cerro Campana, cloud forest, 1000 m, *Croat 22813* (MO, NA, NY, NY). Near summit, Cerro Campana, along trail to summit, 780–875 m, *Croat 25241* (MO). Cerro Campana area above Su Lin Motel, 3000 ft, *Dwyer & Kirkbride 7841* (MO, PMA, US). Trail to Cerro Campana, *Kirkbride & Hayden 280* (MO, MO, SCZ). Cerro Campana, cloud forest, 700 m, *Luteyn 995* (DUKE). Cerro Campana, 2000 m, *Weaver & Foster 1687* (DUKE). Cerro Campana, summit and upper trail, *Witherspoon & Witherspoon 8451* (MO, US). VERAGUAS: Río Segundo Brazo, 8 km beyond Escuela Agricola Alto Piedra beyond Santa Fé, 750 m, *Croat 25545* (MO, PMA). Valley of Río Dos Bocas along road between Escuela Agricola Alto Piedra and Calovébora, 15.6 km NW of Santa Fé, primary forest, 450–550 m, *Croat 27687* (MO). Road between Santa Fé and Río Calovébora, 1.8 mi beyond Escuela Agricola Alto Piedra, 735 m, *Croat & Folsom 34259* (MO). 15–20 km NW of Santa Fé, between Escuela Agricola Alto Piedra and Continental Divide, 650–800 m, *Dressler 4726* (F, MO, PMA). Base of Cerro Tuti, 6.5 km from Santa Fé, *Folsom 3012* (MO, MO, US). NW of Santa Fé, 2.7 km from Escuela Agricola Alto de Piedra, on road to Calovébora, *Mori & Kallunki 5342* (MO, US). NW of Santa Fé, 8.8 km from Escuela Agricola Alto de Piedra, Pacific slope, *Mori & Kallunki 6188* (MO, US).

3. BESLERIA*

Besleria L., Sp. Pl. 2: 619. 1753; Gen. Pl., ed. 5, 271. 1754. TYPE: *B. lutea* L.

Eriphia P. Br., Civ. Nat. Hist. Jamaica 270. 1756. TYPE: *E. jamaicensis* Roem. & Schult. = *Besleria lutea* L.

Cyrtanthemum Oerst., Cent. Gesn. 56. 1858. LECTOTYPE: *C. hirsutum* Oerst. = *Besleria cyrtanthemum* Hanst.

Gasteranthopsis Oerst., Cent. Gesn. 55. 1858. LECTOTYPE: *G. glabra* Oerst. = *Besleria glabra* (Oerst.) Hanst.

Parabesleria Oerst., Cent. Gesn. 53. 1858. LECTOTYPE: *P. triflora* Oerst. = *Besleria triflora* (Oerst.) Hanst.

Pseudobesleria Oerst., Cent. Gesn. 54. 1858. TYPE: *Besleria umbrosa* Mart.

Terrestrial, perennial *herbs* or *shrubs* with fibrous roots; stems terete or quadrangular, to 5 m tall, often unbranched. *Leaves* opposite, in equal or un-

* See *Besleria chiriquensis* Wiehl. Selbyana 5: 73. 1978.

equal pairs, elliptic, ovate or lanceolate, membranous to coriaceous, the apex acute to acuminate, the base cuneate or rounded, entire to coarsely dentate, the stomata randomly scattered; petioles short or long. *Inflorescences* axillary, fasciculate, cymose, to subumbellate; peduncles lacking to elongated; bracts absent. *Flowers* rarely solitary; floral tube very short; calyx lobes united at least at the base, or campanulate, urceolate or cyclindric, 5-toothed or parted, imbricate, rounded to acuminate, entire to serrulate, green or colored; corolla yellow, orange, red, or white, erect or oblique in the calyx, the tube usually cylindric, sometimes spurred or gibbous at the base and sometimes ventricose and contacted at the throat, the limb regular or irregular, 5-lobed, entire; fertile stamens 4, didynamous, included, the filaments broad, adnate to the base of the corolla tube, flattened, usually glabrous, the anthers coherent at first, becoming free, the locules confluent at the apex, the staminode occasionally present; disc annular, usually glabrous, entire, sometimes colored; ovary superior, unilocular with the two parietal placentas ovuliferous only on the inner surface or on both surfaces, the stigma stomatomorphic or bilobed. *Fruit* a fleshy globose berry, red, orange, or white, exocarp thick, verrucose or smooth; seeds minute, ellipsoid, numerous, reddish brown, striate.

Besleria is one of the largest genera in the Gesneriaceae with well over 150 species, distributed from México to Brazil and the West Indies from an apparent center in northwestern South America.

Besleria L. was originally named by Plumier in 1703 for Basilius Besler (1561–1629) a botanist and pharmacist in Nürnberg, Germany.

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Skog, L. E. 1973. A new Colombian species of *Besleria* (Gesneriaceae). Phytologia 26: 502–503.

Wiehler, H. 1975. *Besleria* L. and the re-establishment of *Gasteranthus* Benth. (Gesneriaceae). Selbyana 1: 150–156.

a. Calyx lobes equalling or exceeding the corolla, ca. 2 cm long; leaves lacking formicaria.
  b. Leaf blades subcoriaceous, glabrous above; corolla ca. 1 cm long ..... 11. ***B. rara***
  bb. Leaf blades membranous, strigose or hirsute above; corolla ca. 2 cm long ..... 3. ***B. calycina***

aa. Calyx lobes shorter than corolla, often less than 1 cm long, if equalling or exceeding corolla, then leaves bearing formicaria.
  c. Peduncles evident, but sometimes short; leaves sometimes with formicaria, blades with evident marginal teeth.
    e. Calyx lobes suborbicular, obtuse or rounded; corolla fleshy when fresh ..... 5. ***B. formosa***
    ee. Calyx lobes ovate, ovate-lanceolate to linear; corolla membranous when fresh.

f. Stems, peduncles, and leaves glabrescent or glabrous on mature surfaces; leaf blades lacking formicaria; peduncles usually elongate and more than 2 cm long ..... 7. *B. laxiflora*
ff. Stems, peduncles, and leaves hirsute or pilose; peduncles ca. 1 cm long or less.
g. Inflorescences 1–3-flowered; leaves lacking formicaria.
h. Corollas hirsute, ventricose; calyx lobes lanceolate to ovate ..... 9. *B. pauciflora*
hh. Corolla glabrous, slender; calyx lobes oblong ..... 6. *B. hirsuta*
gg. Inflorescences usually of numerous flowers, rarely reduced to a single flower; leaves with formicaria ..... 4. *B. formicaria*
cc. Peduncles lacking (or, if present, then leaves lacking formicaria, margin also entire—*B. formosa*), pedicels often elongated; leaf margins usually entire, rarely with inconspicuous teeth.
i. Flowers one per node; pedicels usually more than 2 cm long; corollas bright orange.
j. Corolla glabrous, fleshy when fresh; calyx lobes suborbicular, obtuse or rounded, entire ..... 5. *B. formosa*
jj. Corolla glabrous or hirsute, membranous when fresh; calyx lobes lanceolate to oblong, often toothed.
k. Corolla tube large and showy, 1.8–2.3 cm long, outside sericeous villous; leaf blades strongly veined, not tuberculate ..... 2. *B. barbensis*
kk. Corolla tube small, ca. 1 cm long, outside pubescent; leaf blades tuberculate, not strongly veined ..... 10. *B. princeps*
ii. Flowers more than one per node and usually aggregated or congested; pedicels often less than 1 cm long; corolla pink, red, yellow or orange.
l. Calyx lobes densely white tomentose.
m. Leaves elliptic, apex acuminate; calyx lobes rounded ..... 1. *B. arborescens*
mm. Leaves ovate to obovate, apex obtuse; calyx lobes lanceolate ..... 12. *B. robusta*
ll. Calyx lobes glabrescent to strigose.
n. Stems thick (6–10 mm); leaves subcoriaceous to coriaceous and strongly veined.
o. Leaves elliptic, usually less than 20 cm long ..... 14. *B. stricta*
oo. Leaves obovate or broadly elliptic, usually much more than 20 cm long.
p. Stem apex densely white tomentose ..... 15. *B. tambensis*
pp. Stem apex at most strigose ..... 8. *B. notabilis*
nn. Stems slender, apex hirsute or strigose; leaf blades membranous, elliptic or obovate, seldom strongly veined.
q. Pedicels 0.8–1.2 cm long; leaf blades 10–23 cm long; stems hirsute well below the apex ..... 6. *B. hirsuta*
qq. Pedicels 1.2–2.3 cm long; leaf blades 6.3–16.1 cm long; stems strigose at apex, glabrescent below ..... 13. *B. solanoides*

1. **Besleria arborescens** Morton, Contr. U.S. Natl. Herb. 29: 20. 1944. TYPE: Panamá, *Wedel 2353* (US, holotype; MO, isotype).

Tree; stems slender, to 5.4 m tall, densely strigose, the apex yellowish subtomentose. *Leaves* opposite, equal; blades elliptic to obovate, subcoriaceous, 12–27 cm long, 2.7–5.7 cm wide, the apex long acuminate, the base acute to cuneate, entire, ciliate, above medium green, glabrous, below light yellowish green, strigose, especially on the veins; petiole sulcate above, 1.2–2.7 cm long, strigose. *Inflorescences* aggregated in the upper leaf axils; peduncles lacking; pedicels short, to 8 mm, densely strigose. *Flowers* few; calyx lobes free, broadly ovate, 4–6 mm long, 3–5 mm wide, the apex rounded, thick, outside white tomentose, inside glabrous; corolla pink, slightly oblique in the calyx, the tube

cylindric, straight, apparently not gibbous or ventricose, ca. 1.5 cm long, ca. 4 mm wide, the outside densely pilose, the inside glabrous but glandular especially near the apex, the limb slightly 2-lipped, ca. 8 mm across, the lobes suborbicular; stamens with the filaments adnate to the base of the corolla tube, flat, glabrous, the anthers orbicular, ca. 2 mm wide, the staminode conspicuous; disc annular, but thick on one side; ovary ovoid, white tomentose, the style pubescent, the stigma obscurely bilobed. *Berry* green when young, globose, densely pubescent.

Besleria arborescens is known only from the type collection from the province of Bocas del Toro.

BOCAS DEL TORO: Chiriquí Lagoon, *Wedel 2353* (MO, US).

2. **Besleria barbensis** Hanst., Linnaea 34: 319. 1865. TYPE: Volcán de Barba, Prov. Heredia, Costa Rica, *Hoffmann 45* (B, probably no longer extant).

B. barbensis var. *hirsuta* Morton, Ann. Missouri Bot. Gard. 29: 38. 1942. TYPE: Panamá, *Allen 1449* (US, holotype).

Herbs; stems slender, ca. 1 m tall, sparsely strigose to hirsute; unbranched. *Leaves* equal in a pair, elliptic to somewhat obovate, 5.8–12.0 cm long, 2.3–5.0 cm wide, membranous, the apex acuminate, the base cuneate, somewhat oblique, serrulate, above dark green, sparsely strigose to hirsute, the veins obvious, below lighter green, strigose or hirsute along the veins; petioles 0.5–3.2 cm long. *Inflorescences* of single flowers in the axils of the opposite leaves; peduncles lacking; pedicels slender, 1.4–3.0 cm long, pilose. *Flowers* zygomorphic, the posterior calyx lobe slightly larger, free, lanceolate to ovate, 8–13 mm long, 4–7 mm wide, the apex acuminate, sharply serrate, pilose or hirsute outside, inside puberulous; corolla yellow orange, slightly oblique in the calyx, the tube slightly saccate at the base, slightly ventricose, ca. 10 mm long, the base ca. 4.5 mm wide, pubescent toward the limb outside, the inside glabrous, the limb bilabiate, to 12 mm across, larger lobes 5–6 mm long, the smaller lobes 3–4 mm long, all orbiculate, nearly erect to patent, the apex rounded, entire to erose; stamens included, the filaments glabrous, the anthers coherent, quadrate, 1–2 mm wide; disc annular, entire; ovary apex and style pilose, the stigma bilobed. Mature *berry* or *seeds* not seen in Panamá material.

Although the two collections of *Besleria barbensis* differ from each other in amount of vestiture, this range of variation can be seen in collections from nearby localities in Costa Rica.

BOCAS DEL TORO: Róbalo Trail, N slopes of Cerro Horqueta, 6000–7000 ft, *Allen 4943* (F, MO, US). CHIRIQUÍ: Trail from Cerro Punta to headwaters of Río Caldera, 2250–2500 m, *Allen 1449* (US).

3. **Besleria calycina** L. Skog, Brittonia 30: 319. 1978. TYPE: Panamá, *Mori & Dressler 7794* (US, holotype; MO, isotype).

Subshrubs; stems erect, to 1 m tall, slender, ca. 5 mm in diam., probably broader near base, internodes to 8 cm long, reddish or green above, strigose to

hirsute, below brown to gray, glabrescent. *Leaves* opposite, subequal to unequal, elliptic to broadly elliptic or obovate, 4.5–10.0 cm long, 2.2–4.2 cm wide, membranous, the apex acuminate, the base cuneate, the margin entire, above dark green, strigose or hirsute, below lighter green, strigillose, especially along the prominent veins; petioles 0.6–2.2 cm long, strigose. *Inflorescences* single flowers in the upper leaf axils; peduncles lacking; pedicels slender, erect, 2.5–4.0 cm long, 1 mm thick, broader toward apex, hirsute. *Flowers* showy; calyx lobes erect, lanceolate, 1.7–2.4 cm long, to 4 mm wide, the apex attenuate, the midvein prominent and thick, the lateral veins parallel, the margin thin, translucent, entire, green, both sides strigillose; corolla orange, equalling or shorter than the calyx lobes, the tube slightly oblique in the calyx, funnelform, ca. 2.2 cm long, 5 mm in diam. at the base, 10 mm in diam. at the throat, slightly ventricose above the middle, the outside pilose or strigose, the inside pubescent, the limb lobes rotund, ca. 7 mm across, entire; stamens included, the filaments curved, adnate to the base of the corolla tube ca. 1 cm, free part ca. 5 mm long, the anthers broadly sagittate, 2 mm long, 3 mm wide; disc annular, surrounding the base of the ovary, irregularly lobed; ovary oblong, 5 mm long, 3 mm in diam., hirsute above the middle, the style, ca. 1.2 cm long, densely puberulent, the stigma stomatomorphic. Mature *berry* and seeds not seen; immature fruit surrounded by the persistent calyx lobes.

Besleria calycina is known only from the cloud forest at 1,200–1,500 m on Cerro Colorado in the province of Chiriquí. This species is distinctive in the long lanceolate calyx lobes which equal or exceed the corolla.

CHIRIQUÍ: Road along ridge, last stream before rising to antenna, Cerro Colorado, 1650 m, *Folsom et al. 4773* (MO, US). Cerro Colorado, 50 km N of San Félix on the continental divide, 1200–1500 m, *Mori & Dressler 7794* (MO, US).

4. **Besleria formicaria** Nowicke, Brittonia 26: 37. 1974. TYPE: Panamá, *Wiehler & Dressler 71280* (MO, holotype; US, isotype).

B. subulata Nowicke, Brittonia 26: 38. 1974. TYPE: Panamá, *Duke & Lallathin 15008* (MO, holotype; F, US, isotypes).

Large terrestrial *shrubs*; stems 1–2 m tall, ca. 1 cm in diam., subsucculent, green to brown, densely hispid with elongate 2–5 mm long hairs, usually unbranched. *Leaves* broadly elliptic to obovate or subpandurate, 9–29 cm long, 4.2–10.5 cm wide, subcoriaceous to membranous, the apex acute to acuminate, the base obtuse, cuneate to subauriculate, rarely oblique, the margin sparsely serrate or dentate, the upper surface medium green, hispid, the lower surface lighter green, densely hispid along the prominent veins; petiole 0.5–3.7 cm long, densely hispid; formicaria on the upper or lower surface of the leaf at the midvein near the base or in the petiole. *Inflorescences* in the upper axils, cymose to subumbellate; peduncles nearly obsolete to 4 cm long, hispid; pedicels 0.3–1.5 cm long, hispid. *Flowers* several per inflorescence, the calyx nearly regular, the lobes free nearly to the base, linear lanceolate, subulate to narrowly ovate, 1.4–3.0 cm long, green, sparsely to densely hispid, especially at the margins; corolla white, pale yellow, yellow orange to orange, rarely pale lavender, slightly oblique in the calyx, the tube regular, gibbous or saccate at the base, not ventricose above, 1.7–2.4 cm long, ca. 5 mm wide, sparsely pubescent below, pilose near the limb, the inside puberulent, the limb nearly regular, ca. 1 cm across, the lobes more or less

patent, rotund, 3–5 mm long, rarely spotted purple; stamens included, the filaments nearly as long as the corolla, sparsely puberulent, the anthers broader than long, apically coherent; disc more or less annular, but greatly enlarged on one side; ovary ovoid, sparsely pilose at the apex, the style glabrous; stigma capitate. *Berry* globose, 0.6–1.0 cm long.

Besleria formicaria and *B. subulata* were originally described from material from nearby localities in Coclé near El Valle. The distinguishing characters listed in the original publication are so close that one might expect similar extremes within the limits of variability of a single species. One finds as wide a variation in peduncle length, width and shape of calyx lobe between the two species as in other species of *Besleria* when one has more than a few specimens.

The location of the formicaria on the leaves is adaxial or abaxial, as mentioned on the labels of the type specimens, and is probably due to the proclivity or opportunism of the inhabiting ants rather than any consistent differences or preadaptation among the plants.

Besleria formicaria has been found as a terrestrial plant in wet locations in cloud forests in the provinces of Bocas del Toro, Coclé, Los Santos, Panamá, San Blas, and Veraguas.

BOCAS DEL TORO: Between Buena Vista coffee finca and Cerro Pilón, Chiriquí Trail, *Kirkbride & Duke 693* (MO, NY, REED, REED). COCLÉ: La Mesa above El Valle, junction with road to Cerro Pilón, 800 m, *Croat 25413* (MO, PMA). La Mesa above El Valle de Antón, ca. 2 km W of Cerro Pilón on slopes of steep knifelike ridge, 900–930 m, *Croat 37494* (MO). El Valle, 800–1000 m, *Duke 13177* (MO). Cerro Pilón, El Valle, 3000 ft, *Duke & Lallathin 15008* (MO, US). Cerro Gaital Caracoral, 2700–3200 ft, *Dwyer 8915* (MO). Cerro Pilón, hill below summit, above El Valle de Antón, 2000–2700 ft, *Dwyer et al. 4543* (MO). Rivera's sawmill, El Petroso, 7 km N of El Copé, Alto Calvario, 900 m, *Folsom 1345, 3167, 3205, 3232* (all MO, US). La Mesa at El Valle de Antón, *Folsom & Butcher 2840* (MO). El Petroso, summit of mountain, Alto Calvario, *Folsom & Collins 1566* (MO, US). La Mesa above El Valle, 900 m, *Gentry 7440* (MO). El Valle site area of WEPCOR, Cerro Pilón, *Kirkbride 1074* (MO, MO, NY). Mountains N of El Valle de Antón, 2500–3000 ft, *Lewis et al. 1726* (MO). Cerro Pilón, 5 km NE of El Valle, 800–1045 m, *Mori 6589* (MO). La Mesa, 4 km N of El Valle, 850 m, *Nee & Dwyer 9194* (MO, US). El Petroso at Rivera's sawmill, 7 km beyond El Copé, 800 m, *Skog et al. 4192* (E, MO, US), *4208* (MO, P, US). El Valle, *Wiehler & Dressler 71179* (US). Hills just N of El Valle, *Wiehler & Dressler 71279* (US), *71280* (MO, US). LOS SANTOS: Cerro Pilón, rain forest, 2700 ft, *Dwyer & Lallathin 8657* (MO). PANAMÁ: Campo Tres, beyond Cerro Jefe, 700 m, *Croat 27094* (MO). SAN BLAS: Forest SE of Puerto Obaldía, *Croat 16831* (US). VERAGUAS: 5 mi W of Santa Fé on road past Escuela Agricola Alto Piedra on Pacific side of divide, 800–1200 m, *Croat 22993* (MO, PMA). Caribbean slope above Río Primero Brazo 5 mi NW of Santa Fé, 700–1200 m, *Croat 23219A* (MO). Río Primero Brazo, 2.5 km beyond Agriculture School Alto Piedra near Santa Fé, 700–750 m, *Croat 25489A* (MO). Río Dos Bocas, ca. 12 km beyond Santa Fé, 450 m, *Croat 25810* (MO). Between Escuela Agricola Alto Piedra above Santa Fé and Río Dos Bocas ca. 5–8 km from Escuela, 730–770 m, *Croat 25936* (MO). Valley of Río Dos Bocas along road between Escuela Agricola Alto Piedra and Calovébora, 15.6 km NW of Santa Fé, 450–550 m, *Croat 27658* (MO). 0.6 mi beyond Escuela Agricola Alto Piedra, 730 m, *Croat & Folsom 34014* (MO). Banks of first river on road between Alto Piedra School and Río Calovébora, 1.8 mi beyond school, 500 m, *Croat & Folsom 34108* (MO). Guabal, Río Dos Bocas, ca. 16 km NW of Santa Fé, 500 m, *Dressler 5027* (PMA). 6.4 km outside of Santa Fé on the road toward the cordillera, *Folsom 2962* (MO, US). Base of Cerro Tuti, 6.5 km outside Santa Fé, *Folsom 3040* (MO, US). Mountains 3–5 mi N of Santa Fé, 500–1000 m, *Gentry 3021* (MO). 700–1200 m, on Caribbean slope above Río Primero Brazo 5 mi NW of Santa Fé, *Liesner 808* (MO). NW of Santa Fé, 10.8 km from Escuela Agricola Alto de Piedra, on road to Calovébora, *Mori 6718* (MO). Road from Santa Fé to Calovébora 16 km from Santa Fé on Atlantic slope near Río Caloveborita, *Mori et al. 6695* (MO). N of Santa Fé, ca. 2 km N of Escuela Agricola Alto de

Piedra, *Mori & Kallunki 2561* (MO). NW of Santa Fé, 4.2 km from Escuela Agricola Alto de Piedra, *Mori & Kallunki 4834* (MO). NW of Santa Fé, 8.8 km from Escuela Agricola Alto de Piedra, Pacific slope, *Mori & Kallunki 6179* (MO, US). 7 km W of Santa Fé on new road past agricultural school, 2900 ft, *Nee 11188* (MO, US). First branch of Río Santa Maria, roadside and forest a short way S of river, road from Santa Fé, *Witherspoon & Dressler 8921* (MO).

5. **Besleria formosa** Morton, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1151. 1938. TYPE: Yerba Buena, NE of San Isidro, Prov. Heredia, Costa Rica, *Standley & Valerio 49926* (US, holotype).—FIG. 3.

B. amabilis Morton, Contr. U.S. Natl. Herb. 26: 440. 1939. TYPE: Panamá, *Pittier 3239* (US, holotype).

Low *herbs* to *shrubs* to 3 m tall, terrestrial or rarely epiphytic; stems angulate, erect, younger branches sparsely strigose, glabrescent, the internodes often short. *Leaves* lanceolate to elliptic, 3–13 cm long, 1.5–5.0 cm wide, membranous, apex acute to acuminate, the base obtuse to cuneate, entire to sparsely dentate, both the surfaces glabrate or sparsely pubescent on the veins, above dark green, below lighter green; petioles to 5 cm long, sparsely strigose. *Inflorescences* axillary, umbellate when more than 1-flowered, or a few flowers in a fascicle without an evident peduncle; peduncles seldom more than 7 mm long, sparsely strigose to glabrous; pedicels 1.5–4.0 cm long, sparsely strigose to glabrous. *Flowers* with a broad receptacle; calyx lobes briefly connate at the base, fleshy, ovate or orbicular, pale green, sparsely strigose to glabrous, the apex obtuse, ciliate at the margin; corolla bright orange to orange red, fleshy, erect in the calyx, glabrous or sparsely pubescent, the tube more or less cylindric, slightly gibbous at the base, broad, 9–13(–19) mm long, ca. 6 mm wide at the base, slightly broader above, the limb weakly zygomorphic, spreading, 2 upper lobes ca. 4 mm long, 5 mm wide, 3 lower lobes slightly smaller, obtuse, entire, ciliate; stamens included, glabrous, the filaments adnate to the base of the corolla tube, broad at the base, slender toward the apex, curved, ca. 6 mm long, the anthers coherent; disc annular; ovary glabrous at base, pubescent above, the style puberulent, ca. 4 mm long, the stigma 2-lobed. *Berry* globose to oblate, surrounded by the persistent calyx, ca. 8 mm in diam., 6 mm long; seeds ellipsoid to rhombic, obliquely striate, dark brown.

Besleria formosa, known previously only from Costa Rica, here includes the Panamanian *B. amabilis* considered distinct by Morton. The distinguishing characters of glabrous ovary and corolla in *B. formosa* and pilose ovary and corolla in *B. amabilis* blur when one examines the more recently collected material. The full range from glabrous to pilose can be seen in fresh and herbarium material from both countries. The number of flowers in an axil may be from one to few.

In Panamá the species can be found in damp open forests or trailsides at upper elevations in the provinces of Bocas del Toro, Chiriquí, and Veraguas.

A species that resembles *Besleria formosa* and may be confused with it is *B. solanoides* which may be found in the same or nearby localities. The latter species differs from *B. formosa* in having longer internodes, inflorescences lacking a peduncle, and flowers with a narrower calyx and corolla tube.

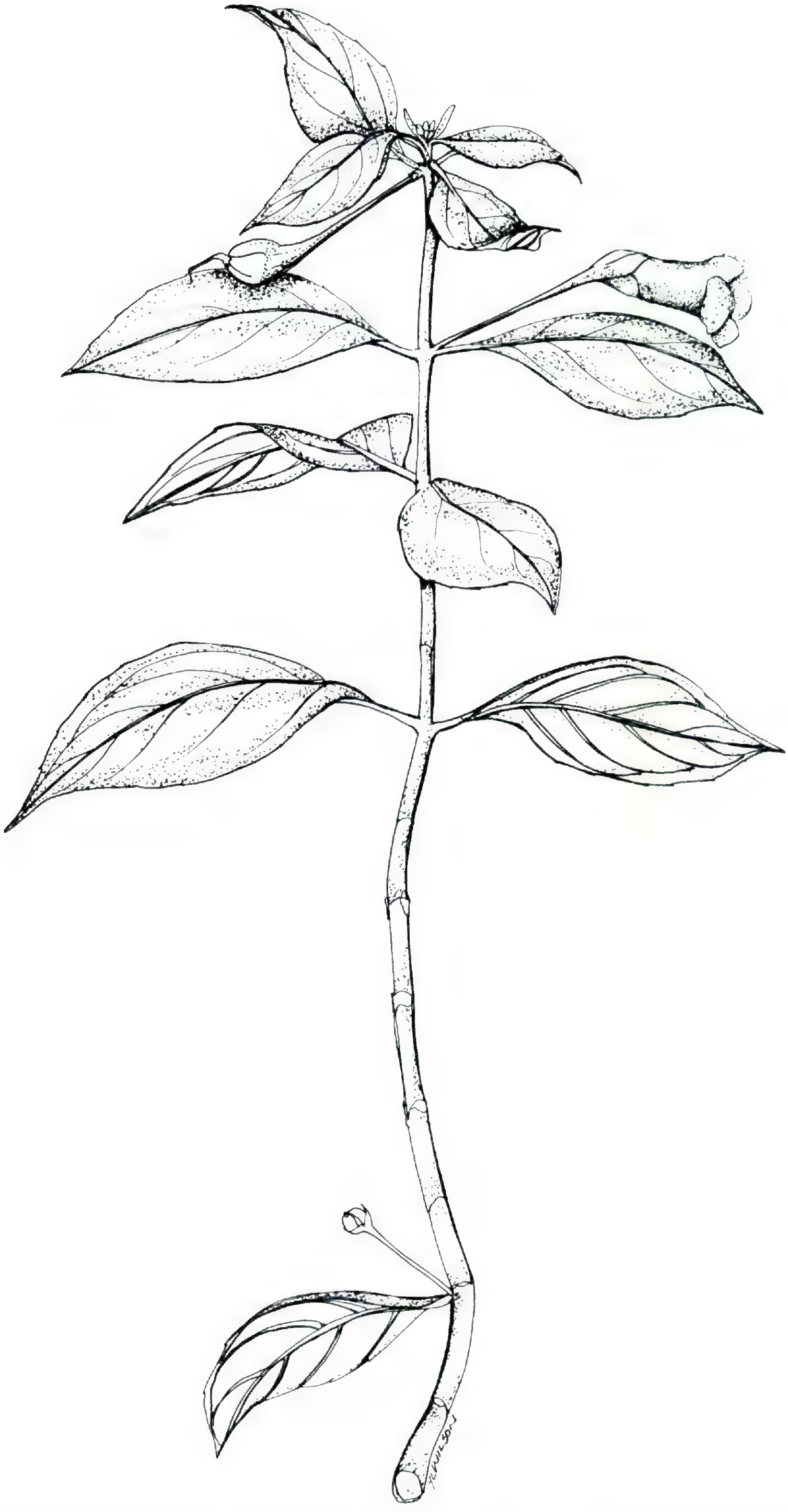

FIGURE 3. *Besleria formosa* Morton. Habit (×7/10). [After *Skog & D'Arcy 4098* (US).]

BOCAS DEL TORO: Róbalo Trail, N slopes of Cerro Horqueta, 6000–7000 ft, *Allen 4961* (MO, US). CHIRIQUÍ: Bajo Mono-Róbalo Trail, western slopes of Cerro Horqueta, *Allen 4822* (MO, US, US). Las Nubes, 2.7 mi NW of Río Chiriquí Viejo W of Cerro Punta, 2200 m. *Croat 22379* (MO, NA). Bajo Chorro, Boquete District, 6000 ft, *Davidson 42* (F, MO, US). Cerro Pando, on the Panamá-Costa Rica border, ca. 16 km NW of El Hato del Volcán, 2000–2482 m, *Mori & Bolten 7273* (MO). Cuesta de Las Palmas, S slope of Cerro de la Horqueta, 1700–2100 m, *Pittier 3239* (US), *sn* (US). Bajo Chorro, near Río Caldera, lower montane rain forest, 1900 m, *Skog & D'Arcy 4098* (E, MO, PMA, P, US). Bajo Chorro trail between 1 and 2.5 hours out of Boquete, 1600–1800 m, *Utley et al. 267* (MO). NW side of Cerro Punta beyond Las Nubes, 7500 ft, *Wilbur & Teeri 13207* (DUKE, MO). S slopes of Cerro Horqueta N of Boquete, 7200 ft, *Wilbur et al. 13483* (DUKE, MO). VERAGUAS: Cerro Tute, 8–10 km NW of Santa Fé, 1200–1300 m, *Dressler 5059* (MO, PMA). Ridgetop, Cerro Tute, ca. 10 km NW of Santa Fé, above 1000 m, *Mori 6780* (MO). Ridge top below summit of Cerro Tute NW of Santa Fé 2 km from Escuela Agricola Alto de Piedra, *Mori & Kallunki 5278* (MO).

6. **Besleria hirsuta** (Oerst.) Hanst., Linnaea 34: 326. 1865.

Gasteranthopsis hirsuta Oerst., Cent. Gesn. 55, *pl. 10, fig. 1–8*. 1858. TYPE: Pedro Tapinapa, Chinantla, México, *Liebmann 9329* (C, holotype; US, photos).

Shrubs; stems erect, 1–3 m tall, slender, ca. 6 mm in diam., hirsute, internodes to 10 cm long. *Leaves* large, oblong or elliptic, 10–23 cm long, 4–10 cm wide, the apex acuminate, the base obtuse to cuneate, sometimes oblique, serrulate, above dark green, sparsely hirsute, below lighter green, hirsute or pilose especially along the veins; petioles elongate 2–8 cm long, 1–3 mm in diam., densely pilose. *Inflorescences* in the upper leaf axils, few-flowered; peduncles short or lacking; pedicels 0.8–1.2 cm long, sparsely pilose. *Flowers* with the sepals briefly connate at the base, the lobes oblong or suborbicular, ca. 5 mm long, membranous, rounded, sparsely pilose; corolla orange or orange red, glabrous, slightly oblique in the calyx, the tube cylindric, slightly saccate at the base, ventricose below the limb, 1.2–1.8 cm long, ca. 3 mm wide at the base, the limb slightly expanded, the lobes suborbiculate, 1–2 mm long; disc annular; ovary glabrous, the style minutely puberulent. *Berry* ovoid to globose, surrounded by the persistent calyx, 7–10 mm long, and wide; seeds ellipsoid, dark reddish brown.

Besleria hirsuta has a disjunct distribution, known from México, Costa Rica and Panamá. It should be expected in Guatemala. *Besleria flava* and *B. conspecta* from Guatemala are similar, differing in having entire leaves and yellow corollas. Within Panamá this species has been found in the provinces of Chiriquí and Darién.

CHIRIQUÍ: Barriles, 6–16 km S of Volcán, 1000–1300 m, *Dressler & Williams 3988* (PMA). 2.5 km from Questa Piedra along Río Monte road, *Folsom 3990* (MO, US). Roadside from Paso Canoas to Cañas Gordas, 1–8 mi from Paso Canoas, *Liesner 222* (US). 17 km NE of San Félix on new road to Cerro Colorado copper mines, 1000 m, *Nee 10708* (MO, US). DARIÉN: Slopes of Cerro Chucula, drainage of Río Pavarandó, *Gentry 4245* (MO). Manené to mouth of Río Cuasí, *Kirkbride & Bristan 1442* (MO, REED), *1546* (MO). Banks above Río Paca, *Stern et al. 596* (MO, US).

7. **Besleria laxiflora** Benth., London J. Bot. 5: 361. 1846. TYPE: British Guiana, *Schomburgk* (K, holotype; photo, US).

B. chiapensis T. S. Brandeg., Univ. Calif. Publ. Bot. 6: 64. 1914. TYPE: Finca Mexiquito, Chiapas, México, *Purpus 7003* (UC, holotype; BM, F, MO, NY, UC, US, isotypes).

B. debilis Rusby, Descr. New S. Amer. Pl. 123. 1920. TYPE: Santa Marta below Valparaiso, Colombia, *Smith 1399* (NY, holotype; BM, K, isotypes).
B. tenuifolia Rusby, Descr. New S. Amer. Pl. 124. 1920. TYPE: Santa Marta near the coast at Don Diego, Magdalena, Colombia, *Smith 2672* (NY, holotype; K, isotype).

Low *shrubs*, suffrutescent *herbs* or rarely small *trees*, terrestrial or rarely epiphytic; stems more or less erect, 0.5–4(7) m tall, slender, young stems fleshy, strigose at the apex, sparsely branched. *Leaves* nearly equal in a pair, elliptic, narrowly oblong, or rarely ovate, 8–21 cm long, 3.0–8.5 cm wide, chartaceous, apex acuminate, the base cuneate, the margin serrate or serrulate, above dark green, sparsely strigillose on the midvein to glabrate, below paler, sparsely pubescent on the veins; petioles 1.5–7.0 cm long, pubescent. *Inflorescences* umbellate to cymose, axillary, flowers few to several; peduncles slender, 1.0–4.5 cm long, pubescent; pedicels often equalling the peduncles, 1–4 cm long. *Flowers* often yellow or orange, calyx actinomorphic, the lobes nearly distinct from the base, ovate to narrowly lanceolate, 5–14 mm long, the apex mucronate, entire to minutely fimbriate or ciliate, green to yellow or orange, glabrescent; corolla variously colored, yellow, orange, salmon red, pink to golden red, erect in the calyx, the tube cylindric, not saccate at the base, but slightly ventricose above, 1.8–2.5 cm long, the outside glabrous, the inside with a pubescent ring near the attachment of the filaments, the limb regular, the lobes ovate, rounded, ca. 2 mm long; stamens included, the filaments curved, glandular, the anthers ca. 2.5 mm wide, coherent; disc annular, irregularly lobed; ovary ovoid, glabrous, style ca. 8 mm long, puberulent, the stigma bilobed. *Berry* orange or red, globose to ovoid, apiculate, 7–12 mm long; seeds ellipsoid, diagonally striate, tawny.

Besleria laxiflora has an extensive range from México, through Central America to Colombia, Venezuela, the Guianas and Brazil. In Panamá it can be found from low to middle elevations in damp deeply shaded woods, near streams and occasionally on rocky banks, in the provinces of Bocas del Toro, Chiriquí, Coclé, Darién, Panamá, and the Canal Zone.

BOCAS DEL TORO: Quebrada Huron, 300–400 ft, *Kirkbride & Duke 440* (MO, NY, REED). 10–15 mi inland (S) from mouth of Changuinola River, *Lewis et al. 880* (MO). Changuinola to 5 mi S at junction of Río Terebe, 100–200 ft, *Lewis et al. 930* (MO). Chiriquicito to 5 mi S along Río Guarumo, *Lewis et al. 2029* (GH, MO, US). Sibubi Falls, Sixaola Valley, *Rowlee & Rowlee 375* (NY, US). Water Valley, *Wedel 709* (MO), *912* (MO, US). Chiriquí Lagoon, *Wedel 1026* (MO, US). Water Valley, Chiriquí Lagoon, *Wedel 1597, 1646* (both MO). Old Bank Island, Chiriquí Lagoon, *Wedel 2138* (MO, US). Fish Creek Mountains, Chiriquí Lagoon, *Wedel 2321, 2340* (both MO, US). Fish Creek Hills, Chiriquí Lagoon, *Wedel 2453* (MO, US). Nievecita, 0–50 m, *Woodson et al. 1826* (MO, US). CANAL ZONE: Navy Reservation N of Gamboa, Río Macho, *Dressler 2916* (DUKE, MO, PMA). NW shore of Canal along road to Achiote, *Folsom 3870* (MO, US). Río Providencia 3 km SE of Achiote near W border of Canal Zone, 5–100 m, *Gentry & Nee 8661* (MO). Río Providencia and ridge S of river, 5–170 m, *Gentry & Nee 8739* (MO, US). N of Frijoles, 30 m, *Killip 3440* (MO, US). Between Frijoles and Monte Lirio, 30 m, *Killip 12146* (PH, US). Pipeline Road N of Gamboa, *Luteyn & Foster 1528* (DUKE). Río Mendosa and small tributary, ½–1 km upstream from Pipeline Road bridge, 8 km NW of Gamboa, 100 m, *Nee 7727* (MO, US). Quebrada San Antonio, 2–3½ km N of Gamboa, 30–200 m, *Nee 9460* (MO, US). Río Mendosa above first gorge, ½–2 km upstream from Pipeline Road bridge, 8 km NW of Gamboa, 100–135 m, *Nee & Smith 11375* (MO, US). Railroad relocation between Gorgona and Gatún, 10–50 m, *Pittier 2282* (US). Hills N of Frijoles, *Standley 27562* (US). 12 mi S of Colón on Río Providencia, *Tyson & Blum 3945* (FSU, MO, SCZ). 12 mi S of Colón, *Tyson et al. 4483* (MO). CHIRIQUÍ: 10–11 mi W of Puerto Armuelles in vicinity of San Bartolo Limite, 300–500 m, *Croat 21992* (MO).

Road from Puerto Armuelles to San Bartolo Limite, 7 mi W of Puerto Armuelles, 120 m, *Croat 35073* (MO). Burica Peninsula, Quebrada Mérida, 4 mi S of Puerto Armuelles, 0–100 m, *Liesner 374* (DUKE, MO, US, USF). Valley of the upper Río Gariché, 1050–1100 m, *Seibert 361* (MO, US). San Bartolomé, Peninsula de Burica, 0–50 m, *Woodson & Schery 905* (MO, NY, US). COCLÉ: El Valle de Antón, Río Indio trail, 500–700 m, *Hunter & Allen 329* (MO). Road from El Valle to La Mesa, 2400–2600 ft, *Vaughan et al. 609* (MO). Headwaters of Río Guaybo, W slopes of Cerro Pajita, 700 m, *Webster 16819* (MO). DARIÉN: Cerro Pirre, *Bristan 509* (MO). Río Yape, *Bristan 1384* (MO). Río Uruceca, *Bristan 1437* (MO). 10 mi S of El Real on Río Pirre, *Duke 5424* (MO). Río Sambú between Sambú and Río Venado, *Duke 9305* (MO, US). Tumaganti, 300 m, *Duke 14162* (MO, USF). Río Perrecenico off Río Pirre, *Duke & Bristan 8233* (MO), *8234* (MO). Between Paya and Palo de las Letras, *Duke & Kirkbride 14048* (MO, SCZ). Cerro Tacarcuna S slope, 1250–1450 m, *Gentry & Mori 13930* (MO). Mannené to the mouth of the Río Cuasí, *Kirkbride & Bristan 1479* (MO, NY, REED). Upper Río Tuquesa, *Le Clezio 173* (MO). Río Tuquesa, at middle Tuquesa Mining Company camp called Charco Peje, 250 m, *Mori 7019* (MO). 4½ km S of El Real, foothills of N slope of Cerro Pirre, *Mori & Kallunki 5403* (MO, US). Boca de Pauarandó, on Sambú River, 20 m, *Pittier 5587* (US), 1912 (US). Banks of Río Paca, *Stern et al. 706* (MO, US). On Río Paca, *Stern et al. 716* (MO, US). Above Paca, *Williams 731* (NY, US). PANAMÁ: Hills above Campana, 600–800 m, *Allen & Alston 1864* (MO). 5 mi above Panamerican Highway on road to Cerro Azul, *Croat 11502* (F, MO). Cerro Azul, *Croat 17303* (F, MO, NY). Altos de Pacora, 20–24 km NE of Cerro Azul, *Dressler 4609* (F, MO, PMA). Goofy Lake to 1.5 mi S of Goofy Lake, 1800 ft, *Dwyer 4394B* (MO), *Dwyer & Hayden 8045* (MO). SE slopes of Cerro Trinidad, *Kirkbride & Duke 1682* (MO, MO, NY, REED). Chimán, *Lewis et al. 3268* (DUKE, MO, PMA). Ridge, Gorgas Memorial Labs yellow fever research camp, ca. 25 km NE of Cerro Azul on Río Piedras, 550 m, *Mori & Kallunki 3290* (MO, US). Junction of Ríos Pacora & Corso to headwaters of Río Corso, *Oliver 2379* (GH, MO, US).

8. **Besleria notabilis** Morton, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1153. 1938. TYPE: La Palma, Prov. San José, Costa Rica, *Wercklé 11603* (US, holotype).—FIG. 4.

B. subdecurrens Morton, Contr. U.S. Natl. Herb. 29(1): 29. 1944. TYPE: Panamá, *Wedel 1926* (US, holotype; MO, isotype).

Coarse *shrubs*; stems woody, 0.5–2 m tall, ca. 1 cm in diam. below, younger stems appressed pubescent, older stems angular, glabrescent. *Leaves* at the stem apices, elliptic to obovate, 13.9–30.5 cm long, 3.9–12.8 cm wide, the apex acute to acuminate, the base acute, obtuse to decurrent, entire to sparsely serrate, coriaceous, above dark green, glabrous, below lighter green and pubescent at the margins and the veins; petioles stout, 1.5–4.5 cm long, ca. 3 mm wide, sparsely pubescent. *Inflorescences* axillary, flowers many per axil; peduncles not evident; pedicels slender, 0.9–1.6 cm long, longer in fruit, pubescent. *Flowers* with the calyx actinomorphic, the sepals distinct, narrowly ovate, 3–5 mm long, ca. 2 mm wide, sparsely pubescent, the margins thin, entire but ciliate, obtuse, reddish, sparsely pubescent outside, the inside glabrous; corolla cream yellow, orange, or red (Wedel), membranous and nearly transparent, slightly oblique in the calyx, the outside sparsely pilose to glabrous, the tube slender, 10–12 mm long, 2–3 mm wide, more or less cylindric with a slightly gibbous base, slightly ventricose above, the limb small, the lobes obtuse, 1–3 mm long; filaments nearly straight, ca. 8 mm long, yellow, glabrous, the anthers suborbicular, ca. 1 mm long, coherent; disc annular or interrupted, glabrous; ovary minutely puberulent; style pilosulus, the stigma bilobed. *Berry* green to white, surrounded by the purplish persistent calyx, globose to oblate, 4–6 mm in diameter; seeds oblong, diagonally striate, shiny, tawny.

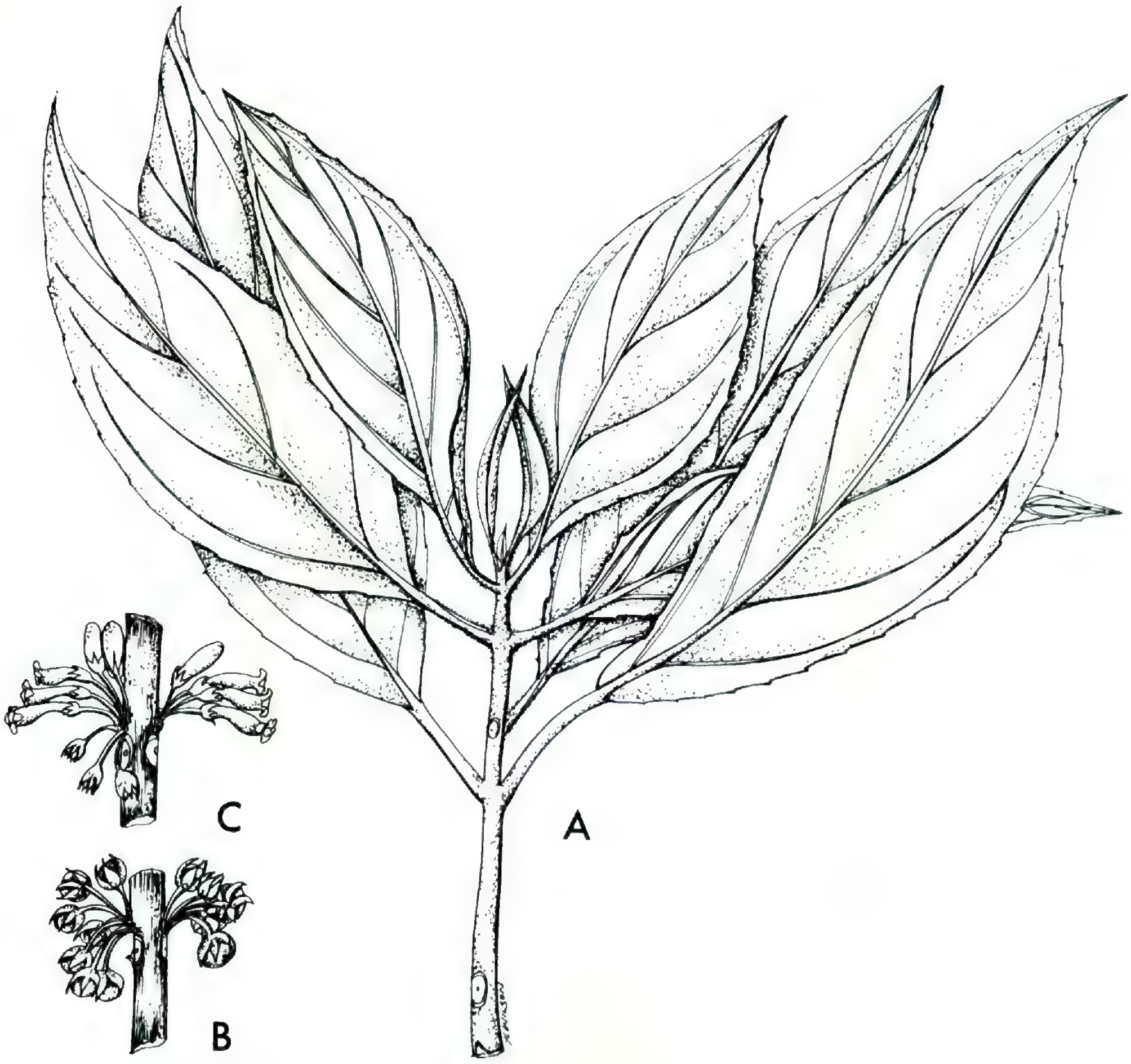

FIGURE 4. *Besleria notabilis* Morton—A. Habit (×⅗).—B. Fruit (×⅗). [After *Dwyer et al. 4507* (MO).]—C. Flowers (×⅗). [After *Witherspoon & Dressler 8900* (MO).]

This species is known from Costa Rica and Panamá. It grows in damp shaded open forests as an understory shrub. *Besleria notabilis* resembles *B. robusta* in the coriaceous leaves, but differs in the smaller and less pubescent calyx, and in the nearly transparent corolla.

BOCAS DEL TORO: Cricamola Valley, region of Almirante, *Cooper 197* (F, NY). E slope of La Zorra to divide, *Kirkbride & Duke 834* (MO, REED). Water Valley, Chiriquí Lagoon, *Wedel 1464* (MO, US, US). Old Bank Island, Chiriquí Lagoon, *Wedel 1926* (MO, US). CHIRIQUÍ: Ridge road at Cerro Colorado, 7.6 km from main road along stream, 1450–1750 m, *Folsom et al. 4828* (MO, US). COCLÉ: Summit of Cerro Pilón, above El Valle de Antón, 2700 ft, *Dwyer et al. 4507* (MO). Alto Calvario, forest around Rivera sawmill, 700–900 m, *Folsom 3245* (MO). El Valle site area of WEPCOR, Cerro Pilón, *Kirkbride 1070* (MO). Cerro Caracoral, *Kirkbride 1120* (MO, MO, NY). Cerro Pilón, 900–1173 m, *Liesner 779* (US). El Petroso, at Rivera's sawmill, 7 km beyond El Copé, 800 m, *Skog et al. 4206* (MO, US). VERAGUAS: Santa Fé, slopes of Cerro Tute, 2500 ft, *Allen 4373* (F). 5 mi W of Santa Fé on road past Escuela Agricola Alto Piedra on Pacific side of divide, 800–1200 m, *Croat 22992* (US). Caribbean slope above Río Primero Brazo 5 mi NW of Santa Fé, 700–1200 m, *Croat 23136* (US). Road between Santa Fé and Río Calovébora, 1.8 mi beyond Escuela Agricola Alto Piedra, 735 m, *Croat & Folsom 34269* (MO). Caribbean slope above Río Primero Brazo 5

mi NW of Santa Fé, 700–1200 m, *Liesner 956* (US). 10 km NW of Santa Fé, road to Calovébora first branch of Río Santa María, *Mori & Bolten 7614* (MO). NW of Santa Fé, 8.8 km from Escuela Agricola Alto de Piedra, Pacific slope, *Mori et al. 3972* (MO), *4008* (MO). 6–7 km W of Santa Fé on new road past agricultural school, 2900 ft, *Nee 9709* (MO, US), *11213* (MO). Second branch of Río Santa María, road from Santa Fé, *Witherspoon & Dressler 8900* (MO). Trail up E side of Cerro Tute, to 1299 m, *Witherspoon et al. 8863* (MO).

9. **Besleria pauciflora** Rusby, Bull. Torrey Bot. Club 27: 31. 1900. TYPE: Mapiri, Bolivia, *Rusby 2437* (NY, holotype; US, photo).

B. pauciflora Rusby var. *uniflora* Morton, Contr. U.S. Natl. Herb. 26(9): 452. 1939. TYPE: Panamá, *Williams 740* (NY, holotype; NY, isotype; US, photo).

B. sprucei Britt. var. *flavescens* Morton, Contr. U.S. Natl. Herb. 38(4): 135. 1968. TYPE: Montenegro, Prov. Bagua, Dept. Amazonas, Peru, *Sagástegui 5867* (US, holotype).

B. wurdackii Morton, Contr. U.S. Natl. Herb. 38(4): 146. 1968. TYPE: Left bank of Río Marañon above Cascades de Mayasi, Prov. Bagua, Dept. Amazonas, Peru, *Wurdack 1955* (US, holotype).

Large *herbs* or bushy *shrubs*; stems lax or weak, somewhat succulent, becoming quadrangular when dry, 0.6–2.0 m tall, hirsute to densely strigose or pilose, pale brown; branched. *Leaves* equal to unequal, ovate to elliptic, 5–21 cm long, 4–9 cm wide, chartaceous when dry, the apex acute to acuminate, the base acute, obtuse to rounded, sometimes oblique, serrate, the upper surface dark green and pilose above, the lower surface lighter green and densely hirsute especially on the prominent veins; petioles 1–5 cm long, hirsute. *Inflorescences* of 1-few flowers in the upper leaf axils; peduncles slender, 0.3–3(–5.6) cm long, sparsely pilose to strigose, hairs dense at the junction of the peduncle to the pedicel in single-flowered inflorescences; pedicels 1.0–2.7 cm long, sparsely pilose. *Flowers* with the calyx more or less regular, campanulate, the lobes distinct nearly to the base, lanceolate to ovate, often elongate, to 1 cm long, green, outside pilose, inside usually sparsely pilose at least near the apex; corolla yellow, yellow orange to red orange with the 2 upper lobes of the limb darker reddish, nearly erect in the calyx, slightly zygomorphic, the tube slightly saccate near the base and somewhat ventricose near the throat, 1.0–2.0 cm long, 3–5 mm wide at the base, to 8.5 mm wide then narrower at the throat, the outside pilose, more or less glabrous within, the limb of 5 rounded lobes, ca. 2 mm long, reflexed, the stamens included, glabrous, the anthers ca. 1.5 mm broad; disc annular, occasionally lobed; ovary pilose, the style 7–8 mm long, pubescent, stigma bilobed. *Berry* oblate or globose, red at maturity, ca. 8 mm long, 1 cm wide, surrounded by the persistent calyx; seeds ellipsoid, ca. 0.5 mm long, obliquely striate, dark brown.

The range of *Besleria pauciflora* extends from Panamá south to Bolivia. The relationship of the Peruvian plants described as *B. wurdackii* Morton and *B. sprucei* var. *flavescens* Morton to those of Panamá can be seen, among other characters, in the darkly colored upper corolla lobes.

The holotype from Bolivia differs from all other material seen of this species mainly in having longer peduncles, to 5.6 cm and longer than the pedicels and stouter. Although the holotype for *B. pauciflora* var. *uniflora* was described as having single flowers, a closer examination of the inflorescences has shown that each bears at least two flowers. This character is even more evident on the isotype sheet.

Plants in Panamá have been collected in wet areas in rain forests or near streams in the provinces of Bocas del Toro, Coclé, Colón, Darién, and Veraguas.

BOCAS DEL TORO: Buena Vista, region of Almirante, *Cooper 226* (NY). Between Quebrada Menaco and Buena Vista on Chiriquí Trail, *Kirkbride & Duke 667* (MO, NY, REED). COCLÉ: Near Río Tucué, above Tucué, by small stream, *Dressler 4197* (PMA). Trail to La Mesa 4.5 mi beyond El Valle de Antón, *Wilbur & Luteyn 11702* (DUKE, DUKE, F, MICH, MO, NY, PMA, US). COLÓN: Cerro Santa Rita, 1200 ft, *Allen & Fairchild 5173* (MO, US, US, US). Río Boquerón, 6–8 km upstream from Peluca Hydrographic Station, *Dressler 4659* (PMA). DARIÉN: Airstrip at Caná gold mine, 480 m, *Croat 37996, 38048* (both MO). Río Cuasí, main stream, 0–2.5 mi S of Tres Bocas, *Kirkbride & Duke 1138* (MO, NY, REED). Caná, 1750 ft, *Stern et al. 494* (MO, US, US). Trail between Caná and Boca de Cupe, 1700 ft, *Stern et al. 680* (MO, US). Caná and vicinity, 2000–6500 ft, *Williams 740* (NY, NY). VERAGUAS: Between Santa Fé and Río Calovébora, 1.8 mi beyond Escuela Agricola Alto Piedra, 735 m, *Croat & Folsom 34260* (MO). Base of Cerro Tuti, 6.5 km outside of Santa Fé, *Folsom 3018* (MO, US). Forest and forest remnants to 12 km NW of Santa Fé de Veraguas, *D'Arcy 10328* (MO). NW of Santa Fé, 217 km from Escuela Agricola Alto de Piedra, on road to Calovébora, *Mori & Kallunki 5343* (MO, US). 16 km NW of Santa Fé, on road to Calovébora, 300–500 m, *Mori & Kallunki 6114* (MO, US). First branch of Río Santa María, S of river, road from Santa Fé, *Witherspoon & Dressler 8907* [probably with wrong label] (MO).

10. **Besleria princeps** Hanst., Linnaea 34: 317. 1865. TYPE: Costa Rica, *Wendland 1273* (B, not seen and probably destroyed).

Terrestrial suffrutescent *herbs*; stems more or less erect, to 3.2 m tall, densely hirsute, hairs uniseriate, brown. *Leaves* well spaced, elliptic or rarely ovate, 7–13 cm long, 3–6 cm wide, membranous, the apex acute, the base acute or cuneate, rarely obtuse, entire to denticulate, the upper surface dark green, hirsute to scabrous, the lower surface lighter green, hirsute and especially dense along the veins; petiole 1.5–4.0 cm long, pilose. *Inflorescences* of a solitary axillary flower; peduncle not evident; pedicels slender, 2.5–4.5 cm long, pilose. *Flowers* showy; calyx weakly zygomorphic, the sepals distinct, narrowly ovate, elongate, erect, 1.5–2.2 cm long, long acuminate, irregularly serrate, densely sericeous to villous outside, glabrous within; corolla orange, erect in the calyx, the tube ca. 1.8 cm long on the anterior side, ca. 2.3 cm long on the posterior side, 5–8 mm wide, the outside pilose, the inside with a pubescent ring near the base, the base not saccate or spurred, expanded in the throat, the limb bilabiate, spreading, 2.0–3.5 cm across, the posterior lobes 0.5–1 cm long and wide, the lateral lobes ca. 1.5 cm long and wide, the anterior lobes ca. 1.2 mm long and wide; stamens puberulent, the filaments convolute, the anthers ca. 3.5 mm wide; disc annular; ovary densely villous, the style ca. 8 mm long, pubescent, the stigma capitate, puberulent. *Berry* not seen.

Although more common in Costa Rica, *Besleria princeps* is rare in Panamá and known only from 2 collections from the province of Chiriquí.

CHIRIQUÍ: Bajo Chorro, Boquete District, 7000 ft, *Davidson 208* (F, MO). Below Divide on Chiriquicito-Calderas Trail, *Kirkbride & Duke 964* (MO).

11. **Besleria rara** L. Skog, Brittonia 30: 320. 1978. TYPE: Panamá, *Witherspoon & Dressler 8893* (US, holotype; MO, isotype).

Shrub; stems short, slender, ca. 5 mm in diam., internodes to 8 cm long, strigose to sericeous near the apex, nearly glabrous below. *Leaves* opposite, nearly

equal in a pair, lanceolate, 5–9 cm long, 1.5–3.2 cm wide, subcoriaceous, the apex acuminate, the base acute or cuneate, entire, above dark green, at first glandular, soon becoming glabrous, below lighter green, sparsely strigillose, veins darker and prominent; petioles 3–8 cm long, strigose. *Inflorescences* in the upper axils, of 1(2) nearly sessile flowers per axil; peduncles lacking; pedicels short, 1–3 mm long, strigose. *Flowers* with the calyx lobes erect, lanceolate, 1.5–1.8 cm long, 2–3 mm wide, the outside strigose, the inside nearly glabrous except at the entire margin, the midvein subprominent, slightly keeled at the base; corolla orange, somewhat oblique in the calyx, the tube ca. 1.1 cm long, narrowly funnelform, 2 mm in diam. at the base, slightly broader, to 4 mm wide above, nearly glabrous at the base, strigillose toward the limb, the inside glandular, the lobes of the limb semiorbicular, ca. 4 mm long, 5 mm wide, subentire, ciliate; stamens included, the filaments curved, adnate to the base of the corolla tube for ca. 3 mm, the free part 4–5 mm long, glabrous, the anthers broadly sagittate, 1.5 mm long, 2 mm wide, coherent in 2 pairs by their apices, staminode 3 mm long, bearing a short infertile anther; disc semiannular at the base of the ovary with a gap on the lower side, irregularly lobed; ovary ovoid, ca. 3 mm long, glabrous, the style 5 mm long, glabrous, the stigma stomatomorphic. *Berry* surrounded by the persistent calyx, ovoid to globose, ca. 1 cm long, white, glabrous, apex prominent; seeds ellipsoid, deeply striate, ca. 0.5 mm long, light brown.

Besleria rara has only been collected once from near the Río Santa María in the province of Veraguas. Although both *B. calycina* and *B. rara* have calyx lobes equalling or exceeding the corolla, *B. rara* has a corolla only ca. 1.1 cm long, abut half the length of the corolla of *B. calycina*. The species also differs in having glabrous, subcoriaceous leaves.

VERAGUAS: Forest near second branch of Río Santa María, road from Santa Fé, *Witherspoon & Dressler* 8893 (MO, US).

12. **Besleria robusta** J. D. Smith, Bot. Gaz. (Crawfordsville) 25: 156. 1898. TYPE: Forests of Taskí, Talamanca, Prov. Limón, Costa Rica, *Tonduz 9556* (CR, holotype; US, isotype).

Coarse terrestrial or rarely epiphytic *shrubs*; stems woody, erect, 0.5 to 3 m tall, terete, to 1 cm thick, younger stems pubescent to tomentose, brown; usually unbranched. *Leaves* ovate to obovate, 12 to 33 cm long, 5 to 17 cm wide, succulent, becoming coriaceous, the apex obtuse, rounded or acute, the base cuneate, entire or sparsely toothed at the distal end, above dark green, glabrous, below pale whitish green, pubescent on the prominent veins and the margins; petioles stout, 2–5 cm long, ca. 5 mm wide, grooved on the upper side, tomentose to sericeous. *Inflorescences* axillary, cymose but aggregated and lacking peduncles or bracts, few flowered; pedicels 6–10 mm long, sericeous. *Flowers* with the calyx actinomorphic, the lobes connate briefly at the base, thick and fleshy, ovate to broadly triangular, 7–12 mm long, ca. 5 mm wide at the base, the apex acute, entire, often orange, sericeous with white to brownish hairs externally, internally glabrous; corolla erect in the calyx, the tube 9–14 mm long, fleshy, usually orange but occasionally salmon yellow, reddish, pale yellow or pinkish,

the outside glabrous but glandular, the inside pilosulus on the upper half, the limb of 5 small lobes, each 2–3 mm long, rounded; stamens with filaments adnate to the base of the corolla tube, yellow, anthers ca. 2 mm long, coherent, staminode ca. 4 mm long; disc annular; ovary glabrous, oblong-conical, style ca. 8 mm long, the stigma capitate to slightly bilobed. *Fruit* globose or ovoid, surrounded by the persistent calyx, ca. 6 mm in diam., yellow, white, orange or brown; seeds oblong, shining, deeply striate, tawny.

This species is endemic to Costa Rica and Panamá where it occurs at middle elevations in the dense shade of wet forests or near streams.

Besleria robusta is part of a complex of species that seem to be closely related because of their subcoriaceous leaves and aggregated flowers. These include *B. arborescens* and *B. notabilis* from Panamá, which differ in having shorter round calyx lobes, *B. aggregata* (Mart.) Hanst. from Peru and Colombia which has elliptic leaves with acute or acuminate apices and bearded corolla lobes, *B. eriocalyx* from Colombia which has a broader corolla, and *B. calantha* Morton from Colombia which has only ciliate calyx lobes. From other species of *Besleria* in Panamá, *B. robusta* is distinctive in its sericeous, broadly triangular or ovate, acute calyx lobes.

BOCAS DEL TORO: Buena Vista Camp on Chiriquí Trail, 1250 ft, *Cooper 584* (F, NY). Above Quebrada Huron on Cerro Bonyic, 500–1200 ft, *Kirkbride & Duke 624* (MO). Without locality, *Wedel 310* (MO). Chiriquí Lagoon, Fish Creek, *Wedel 2184* (MO, US). Fish Creek mountains, Chiriquí Lagoon, *Wedel 2245* (MO, US). Bastimentos "short cut," Chiriquí Lagoon, *Wedel 2912* (MO, US). CANAL ZONE: Headwaters of Río Providencia, 7.5 km SW of Gatún Dam, 25–140 m, *Nee & Gentry 8670* (MO). COCLÉ: La Mesa above El Valle, *Croat 14307* (MO). Hills above El Valle de Antón, *D'Arcy & D'Arcy 6756* (F, MO). Foothills of Cerro Pilón near El Valle, 900 m, *Duke 14664* (MO). La Mesa above El Valle, *Dwyer 11895* (MO, PMA). Cerro Pilón, 2900 ft, *Dwyer & Lallathin 8638* (MO, NY). Summit of Cerro Pilón above El Valle de Antón, 2700 ft, *Dwyer et al. 4483* (MO, SCZ). Base of Cerro Pilón above El Valle, *Gentry & Dwyer 3651* (MO). El Valle de Antón, La Mesa, 1000 m, *Kennedy et al. 3043* (F, MO). Cerro Pilón, 2900 ft, *Lallathin 50003* (MO). Boca del Toabré at confluence of Río Coclé del Norte, *Lewis et al. 5561* (MO, SCZ). 5 mi N of El Valle de Antón, 1000 m, *Luteyn 1209* (DUKE, MO). Road from El Valle to La Mesa, 2400–2600 ft, *Spellman et al. 587* (MO). N rim of El Valle de Antón near Cerro Turega, 650–700 m, *Woodson & Schery 181* (F). COLÓN: Santa Rita Ridge, *D'Arcy & D'Arcy 6135* (MO, NY). DARIÉN: Ascent of Cerro Pirre, from Río Pirre, 750–1030 m, *Duke 5328* (MO). Cerro Pirre, 2500–4500 m, *Duke & Elias 13768* (MO). Summit of Cerro Pirre, 1000–1400 m, *Gentry & Clewell 7114* (MO). PANAMÁ: Cerro Campana, 850 m, *Busey 844* (MO). Cerro Campana along road above FSU cabin, *Croat 14193* (MO), *14210* (MO). Cerro Campana above Su Lin Motel, *Croat 14771* (MO). Cerro Campana along trail to summit, 780–875 m, *Croat 25236* (MO). Cerro Campana area above Su Lin Motel, 3000 ft, *Dwyer & Kirkbride 7847* (MO, SCZ). Capira, NE side of Cerro Trinidad, 900 m, *Foster 2115* (DUKE). Cerro Campana, ca. 1 mi past the Florida State U. Field Station, 800 m, *Kennedy 1542* (MO, US). Trail to Cerro Campana, *Kirkbride & Hayden 270* (MO, MO, NY, SCZ). Cerro Campana, 8.6 mi SW of Capira, 700–800 m, *Luteyn 1019* (DUKE). Cerro Campana, 2900 m, *McDaniel 6863* (FSU). Cerro Campana, N slope, 850 m, *Mori et al. 1921* (MO). Cerro Campana, 800 m, *Skog et al. 4154* (US). Cerro Campana, *Smith & Smith 3394* (F, US). VERAGUAS: Valley of Río Dos Bocas on road between Alto Piedra and Calovébora, 350–400 m, *Croat 27430* (MO). E of river, valley of Río Dos Bocas along road between Escuela Agricola Alto Piedra and Calovébora, 15.6 km NW of Santa Fé, 450–550 m, *Croat 27730* (MO). Mountains 3–5 mi N of Santa Fé, 500–1000 m, *Gentry 2959* (MO). N of Santa Fé, ca. 2 km N of Escuela Agricola Alto de Piedra, *Mori & Kallunki 2588* (MO). NW of Santa Fé, 11 km from Escuela Agricola de Piedra, in valley of Río Dos Bocas, Atlantic slope, 450–550 m, *Mori et al. 3893* (MO). 7 km W of Santa Fé on new road past agricultural school, 2900 ft, *Nee 11203* (MO). First branch of Río Santa María S of river, road from Santa Fé, *Witherspoon & Witherspoon 8910* (MO, US).

13. **Besleria solanoides** Kunth *in* H.B.K., Nov. Gen. Sp. 2: fol. ed. 319; qto. ed. 398. 1818. TYPE: Popayán, Colombia, *Humboldt 2079* (B; US, photo).

Besleria acutifolia Benth., Pl. Hartw. 237. 1846. TYPE: Popayán, Colombia, *Hartweg 1276* (K, holotype; US, photo).
Parabesleria costaricensis Oerst., Cent. Gesn. 53. 1858. TYPE: Turrialba, Costa Rica, *Oersted 9276* (C, holotype; US, photo).
Besleria costaricensis (Oerst.) Hanst., Linnaea 34: 330. 1865.
B. obliqua Morton, Ann. Missouri Bot. Gard. 29: 40. 1942. TYPE: Panamá, *Allen 2396* (US, holotype; MO, isotype).

Suffrutescent *herbs*, small to large *shrubs*, or small *trees*; stems woody, slender, terete, erect, 0.5–5 m tall, when young strigose toward the apex, becoming glabrous with age. *Leaves* elliptic, or sometimes obovate, 6.3–16.1 cm long, 1.9–5.8 cm wide, the apex acute to acuminate, the base cuneate, entire to denticulate, chartaceous to membranous, above dark green, smooth to nearly glabrous or sparsely pilose to scabrous, below lighter green, strigose or strigillose on the veins; petioles 0.6–5.5 cm long, strigillose. *Inflorescences* axillary, flowers fasciculate, few to several per axil; pedicels 1.2–2.3 cm long, pubescent; calyx slightly zygomorphic, lobes distinct nearly to the base, ovate, or oblong, 2–4 mm long, green, sparsely pilose, ciliate; corolla orange or yellow, erect to slightly oblique in the calyx, nearly regular, rarely somewhat calcarate at the base, ventricose anteriorly, 11–15 mm long, ca. 3 mm in diam. near the base, slightly wider above, glabrous to glandular, the limb more or less regular, the lobes ovate, 1–2 mm long, sparsely pubescent; stamens included, 4, the filaments flattened, convolute, glabrous, the anthers sagittate, ca. 1 mm wide; disc annular, sometimes interrupted; ovary more or less glabrous, the style 0.6–1.2 cm long, sparsely pubescent below, the stigma bilobed, flattened at the top, papillate. *Berry* globose, 6–7 mm in diam., red, orange, yellow or white; seeds oblong, dark brown, obliquely striate.

Besleria solanoides has been widely collected from Honduras south to Colombia and Peru. In Panamá it may be found at middle elevations in moist shaded forests usually near streams or rivers.

BOCAS DEL TORO: Róbalo Trail, N slopes of Cerro Horqueta, 6000–7000 ft, *Allen 4985* (MO, US). Río Teribe, foothills of Cerro Bonyic, 400–800 ft, *Kirkbride & Duke 410* (MO, NY, REED). CHIRIQUÍ: Finca Lérida, upper S slopes of Quebrada Velo, 5000 ft, *Allen 4754* (MO, US). Cerro Horqueta, 7000 ft, *Blum & Dwyer 2627* (FSU, MO, SCZ). "Monte Rey" above Boquete, *Croat 15668* (MO, PMA). NW side of Cerro Pando, *Croat 15965, 15992* (both MO). Cerro Colorado, on upper mining road 20–28 mi from San Félix, 1200–1500 m, *Croat 33279* (MO, US). Cerro Colorado, along road to copper mine 43.1 km beyond bridge over Río San Félix near town of San Félix, 1390 m, *Croat 37294, 37297* (both MO). N side of Cerro Pando, 6400 ft, *D'Arcy 5403* (MO, USF). Wet ravine W of Cerro Pando, 6000 ft, *D'Arcy & D'Arcy 6627* (MO). Bajo Chorro, Boquete District, 6000 ft, *Davidson 197* (F, MO, US), *713* (F, MO). Road from Boquete to Finca Lérida, 2000 m, *Dressler & Williams 4010* (DUKE, MO, MO, PMA, US). Boquete, Finca Collins, 5000 ft, *Dwyer & Hayden 7657* (DUKE, MO). Cerro de Horqueta, 4500–5500 ft, *Dwyer & Lallathin 8775* (MO, MO). Boquete, Collins Finca, 6000 ft, *Ebinger 686* (MO, US), *729* (MO). Road from Volcán to Río Sereno, 16.0 km from Río Sereno, *Folsom 4052* (MO, US). Cerro Colorado, border of Chiriquí and Bocas del Toro provinces, 1600–1700 m, *Folsom et al. 4766* (MO, US). Ridge road at Cerro Colorado, 6.2 km from main road, 1450–1750 m, *Folsom et al. 4813* (MO, US). Cerro Horqueta, 6500 ft, *Hagen & Hagen 2049* (MO), *2057* (NY, US), *2077* (NY, US). Finca Collins, 6000 ft, *Kirkbride 118* (MO, NY, SCZ). Cerro Horqueta, 5000–7000 ft, *Kirkbride 138* (F, MO, NY, SCZ). Between Pinola and divide on Chiriquicito-Caldera Trail, *Kirkbride &*

Duke 853 (MO, REED). Chiriquí Trail between Pinola and Quebrada Hondo toward summit, *Kirkbride & Duke 890* (MO, NY, REED). Bajo Mono trail, NW of San Ramón towards the headwaters of the Río Caldera, 1600–1700 m, *Luteyn 3718* (DUKE). Sierra del Boquete, 1200 m, *Maurice 704* (MO, US). Boquete, 1000–1300 m, *Maxon 4953* (F, US). Río Piedras Candella, 1800 m, *McAlpin 2204* (DUKE). Santa Clara region, 27 km NW of El Hato del Volcán, on coffee finca of Rattibor Hartman called Ojo de Agua, 5000–5300 ft, *Mori & Bolten 7196* (MO). Cerro Colorado, 50 km N of San Félix on the continental divide, 1200–1500 m, *Mori & Dressler 7797* (MO), *7812* (MO, US). N of San Félix at Chiriquí-Bocas del Toro border, on Cerro Colorado copper mine road along continental divide, 5000–5500 ft, *Mori & Kallunki 5861* (MO, US). Boquete, 1000–1300 m, *Pittier 2972* (US, US). Valley of the upper Río Chiriquí Viejo, *White 345* (F, MO). San Ramón near Bajo Mono, 4 mi NW of Boquete, 6000 ft, *Wilbur et al. 13545* (DUKE, F, MO, NY). Casita Alta, Volcán de Chiriquí, 1500–2000 m, *Woodson et al. 927* (NA, NY, US, US). Quebrada Velo, 1800 m, *Woodson & Schery 254* (MO, US). Bajo Mono and Quebrada Chiquero, 1500 m, *Woodson & Schery 594* (MO, US). COCLÉ: La Mesa N of El Valle de Antón, 1000 m, *Allen 2396* (MO, US). Cerro Pilón 5 km NE of El Valle, 800–1045 m, *Mori et al. 6550* (MO, US). DARIÉN: Serrania de Pirre, ca. 9 km from Alto de Nique, 1480–1520 m, *Croat 37890* (MO). Cerro Pirre, *Duke 6086* (MO, SCZ, USF), *6087* (MO); *Duke & Elias E13823* (MO, SCZ); 1400 m, *Folsom 4343* (MO, US); *Folsom 4553* (MO, US). Cerro Tacarcuna summit camp, 1500–1750 m, *Gentry & Mori 14038* (MO). Caná, 2000–6500 ft, *Williams 836* (NY). PANAMÁ: Capira, NE side of Cerro Trinidad, 900 m, *Foster 2112* (DUKE, MO). VERAGUAS: 0.5 mi beyond fork in road at Escuela Agricola Alto Piedra on road to Río Calovébora, 750 m, *Croat & Folsom 33861* (MO). 0.6 mi beyond Escuela Agricola Alto Piedra, 730 m, *Croat & Folsom 34078* (MO). Cerro Tute, ca. 10 km NW of Santa Fé, 1000 m, 750–1000 m, *Mori 6253, 6292* (both MO), *Mori et al. 7610* (MO, US). NW of Santa Fé, 2 km from Escuela Agricola Aito de Piedra, *Mori & Kallunki 5290* (MO).

14. **Besleria stricta** L. Skog.[6] TYPE: Panamá, *Nee & Warmbrodt 10346* (US, holotype; MO, isotype).

Coarse *herbs* or *shrubs*; stems strict, 0.25–3.0 m tall, slender, succulent when young, toward the apex green, strigose or sericeous, brown to gray and nearly glabrous below, the internodes often elongate, to 10 cm long; unbranched or once branched. *Leaves* equal in a pair; blades elliptic to oblanceolate, occasionally falcate, 7–19 cm long, 1.3–5.5 cm wide, membranous to subcoriaceous, the apex acute to acuminate, the base cuneate or decurrent into the petiole, entire to remotely and finely denticulate, above dark green to grayish, glabrous or sparsely strigose, below lighter green to purplish at the veins, strigillose, especially along the prominent veins; petioles 0.5–3.5 cm long, strigillose. *Inflorescences* in the upper leaf axils, 1-several flowers in short condensed cymes; peduncles short or lacking; pedicels to 1 cm long, green, sericeous or strigose. *Flowers* with the calyx lobes rotund, ca. 6 mm long, ca. 5 mm wide, white to bluish, outside strigillose to hirsute, inside strigillose to glabrous or glandular, erose, ciliate; corolla orange, the tube oblique in the calyx, cylindric, straight or slightly ventricose above the gibbous base, to 7 mm wide at the middle, the outside strigillose to hirsute above, the inside glandular, the lobes of the limb spreading, rotund, ca. 4 mm long and wide, finely erose, glandular ciliate; stamens included, the filaments curved, broad at the base, adnate to the base of the corolla tube for 5 mm, ca. 5 mm free, glabrous, the anthers 2 mm long, 3 mm wide; disc annular, surrounding the base of the ovary, the ovary sparsely pubescent, the style ca. 1 cm long, pilose, the stigma stomatomorphic. *Berry* globose to broadly ovoid, 8–11 mm long, 8–10 mm in diam., white, glabrous;

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[6] *Besleria stricta* L. Skog, sp. nov. Species insignis caulibus strictis, inflorescentiis congestis, calycis albis vel caeruleis et corollis aurantiacis.

seeds ellipsoid, obliquely striate, ca. 0.5 mm long, brown, attached to a slender white funiculus.

This species is known from the provinces of Darién and Panamá, but may be expected in San Blas and neighboring Colombia. It differs from other species in its strict habit, congested inflorescences, and the combination of orange corolla and white or bluish calyx.

DARIÉN: Headwaters of Río Tuquesa, ca. 2 km air distance from continental divide, upper gold mining camp of Tyler Kittredge, *Croat 27184* (MO). Ascent of Serrania de Pirre above Caná gold mine between Río Caná and Río Escucha Ruido, 1000–1310 m, *Croat 37778* (MO); 1310–1430 m, *Croat 37799* (MO). Between upper Río Membrillo and Camp 7 on the construction road to San Blas, 100–800 m, *Duke 10861, 10898* (both MO). Cuasí-Caná Trail on Cerro Campamiento E of Tres Bocas, headwaters of Río Cuasí, *Kirkbride & Duke 1217* (MO). PANAMÁ: El Llano-Cartí Road 12 km from Panamerican Highway, *D'Arcy 10603* (MO). La Eneida region of Cerro Jefe, *Dressler 4039* (DUKE, F, MO, MO, PMA). El Llano-Cartí highway, 12 km N of El Llano, *Dressler 4669* (PMA). Cerro Jefe, Altos de Pacora, trail to Sebastian's house, 18.2 km E of Cerro Azul Village (Goofy Lake), 800–900 m, *Gentry & Mori 13429* (MO). Ca. 10 km N of Panamerican Highway on El Llano-Cartí Road, 500 m, *Gentry et al. 8877* (MO). Edge of river and cloud forest, Altos del Río Pacora, 2500 ft, *Lewis et al. 2269* (MO). El Llano-Cartí Road, 8–19 km from Panamerican Highway, 400–450 m, *Mori & Kallunki 1846, 2280, 2883, 3504* (all MO); *Nee & Tyson 10950* (MO, US); *Nee & Warmbrodt 10346* (MO, US).

15. **Besleria tambensis** Morton, Contr. U.S. Natl. Herb. 26(9): 428. 1939. TYPE: La Costa, Dist. El Tambo, Dept. El Cauca, Colombia, *Sneidern 850* (S, holotype).

B. crassicaulis Morton, Ann. Missouri Bot. Gard. 29: 39. 1942. TYPE: Panamá, *Terry & Terry 1534* (F, holotype).

Terrestrial *shrubs*; stems thick, erect, 1–2 m tall, ca. 1 cm in diam., somewhat succulent above, densely sericeous, glabrescent below; unbranched or few branched. *Leaves* nearly equal in a pair, broadly elliptic, 17–36 cm long, 7.5–19.3 cm wide, coriaceous, the apex acute to abruptly acuminate, the base acute, obtuse to cuneate, ciliate, entire to sparsely serrate, above dark green and glabrous, below lighter yellowish green, sericeous strigose on the prominent veins; petiole stout, 2.5–4.5 cm long, ca. 5 mm wide, densely sericeous. *Inflorescences* in the upper leaf axils, many flowered; peduncles lacking; pedicels slender, 5–13 cm long, hirsute to pilose. *Flowers* with the calyx regular, the lobes distinct, ovate to rounded, 3.5–5.0 mm long and wide, sparsely to densely pilose outside, glabrous within; corolla orange, scarlet to red, more or less erect in the calyx, the tube membranous, cylindric, slightly gibbous above the base, slightly ventricose above, 15–17 mm long, 3–4 mm in diam. at the base, slightly broader near the limb, sparsely pilose outside, glabrous inside, the limb scarcely broader than the tube, the lobes suborbiculate, ca. 2.5 mm long, entire, the filaments glabrous; disc annular, glabrous; ovary apex sparsely pilose, the style puberulent, the stigma bilobed. *Berry* globose to oblate, 5–7 mm in diam.; seeds oblong, diagonally striate, tawny.

Besleria tambensis was originally described from Colombia but its range includes the Panamanian *B. crassicaulis* from Darién and Panamá. The species can be distinguished by its densely sericeous upper stem and leaf veins.

DARIÉN: Río Cuasí, main stream, 0–25 mi S of Tres Bocas, *Kirkbride & Duke 1137* (MO). 0–2 mi E of Tres Bocas along the shortest headwater of Río Cuasí, *Kirkbride & Duke 1168* (MO, REED). Forest between Tres Bocas and Cerro Campamiento on Cuasí-Caná Trail, *Kirkbride & Duke 1358* (MO). Río Cuasí, *Terry 1530* (MO). Caná-Cuasí Trail, Chepigana District, 2000 ft, *Terry & Terry 1534* (F). PANAMÁ: Gorgas Memorial Labs yellow fever research camp, ca. 25 km NE of Cerro Azul on Río Piedras, 550 m, *Barrett et al. 3435* (MO).

4. CAPANEA

Capanea Decne. ex Planch., Fl. Serres Jard. Eur. 5: *pl. 499–500.* August 1849.
TYPE: *C. grandiflora* (Kunth) Decne. ex Planch.

Terrestrial or usually epiphytic *herbs* or *shrubs* from scaly rhizomes;[7] stems erect, scandent or pendent, terete, brownish from dense reddish brown pubescence. *Leaves* opposite, usually equal in a pair; blades membranous, lanceolate, ovate to elliptic, usually asymmetric from an oblique base or falcate, crenate to serrate, above dark green to reddish brown, densely to sparsely tomentose, rarely scabrous or glabrescent, lighter green or purplish beneath, pubescent to villose especially along the veins, the lateral veins 7–9, arching toward the apex at the margin; petioles to ⅓ the length of the blade, seldom nearly sessile, villous with reddish brown hairs. *Inflorescences* axillary but soon overtopping the stem apex, pendent, cymose or umbellate, with leafy bracts; peduncles and the pedicels elongate, similar to the stem, terete, green to brown, pubescent or villous. *Flowers* 1 to 8 per peduncle, each large and showy, zygomorphic; floral tube turbinate to globose, short until anthesis, sometimes costate, villous; calyx lobes 5, shortly connate at the base, broadly triangular to linear lanceolate, entire, dark green to reddish brown; corolla of 5 connate petals, erect in the calyx, limb 5-lobed, spotted, the tube ventricose, but not spurred, often greenish with lines or spots, pubescent to villous externally; stamens 4, with a reduced staminode, exserted at anthesis, the filaments adnate to the base of the corolla tube, not connate but broadly based, slender above, sometimes coiled, the anthers oblong, divergent, apically coherent, dehiscing by longitudinal slits; disc of 5 large usually free glands; ovary more than half inferior, the style thick, exserted at anthesis, the stigma stomatomorphic, ovules numerous. *Fruit* a dry capsule included in the persistent calyx, globose or ovoid, opening by 2–4 valves; seeds linear, dark brown, obliquely striate.

Capanea is a genus of about 6 species in Central and northern South America. The plants occur as terrestrial herbs or shrubs on banks or as epiphytes in trees. One species grows in Panamá, *C. grandiflora*.

Plants of *Capanea* are probably either hummingbird- or bat-pollinated. Vogel (1958) illustrated *Capanea grandiflora* in his paper on "Bat-flowers" in South America.

There has been a controversy in recent years over the correct spelling of the genus name. Decaisne (1849) spelled the name both *Capanea* and *Campanea*. But according to Denham (1975) the name was consistently spelled *Capanea* in the valid publication of the genus by Planchon. The latter is the spelling

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[7] Rhizomes were not seen in Panamanian material, but Bentham (Gen. Pl. 2: 992. 1876) includes this genus among those with tubers or rhizomes, as have later authors.

adopted here to follow Article 73 of the 1972 International Code of Botanical Nomenclature.

Literature:

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Denham, D. 1966. *Campanea*, an orthographic error for *Capanea* [Gesneriaceae]. Baileya 14: 37–39.
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Morton, C. V. 1973. Lectotypification of *Isoloma* and *Campanea* (Gesn.). Taxon 22: 317–318.
Vogel, S. 1958. Fledermausblumen in Südamerika. Oesterr. Bot. Z. 104: 491–530.

1. **Capanea grandiflora** (Kunth) Decne. ex Planch., Fl. Serres Jard. Eur. 5: *pl. 499–500*. 1849.—FIG. 5.

Besleria grandiflora Kunth in H.B.K., Nov. Gen. 2: fol. ed. 321; qto. ed. 401. 1818. TYPE: Colombia, *Humboldt & Bonpland* (P, not seen; photo US).
Drymonia ?grandiflora (Kunth) G. Don, Gen. Hist. 4: 653. 1838.
Rytidophyllum oerstedii Klotzsch, Allg. Gartenzeitung 20: 17. 1852. TYPE: Costa Rica, *Oersted 9325* (B, holotype destroyed; US, isotype).
R. humboldtii Klotzsch, Allg. Gartenzeitung 20: 18. 1852. TYPE: Veraguas, Panamá, *Warscewicz 26* (B, destroyed).
Capanea oerstedii (Klotzsch) Oerst., Cent. Gesn. 34. 1858.
C. humboldtii (Klotzsch) Oerst., Cent. Gesn. 34. 1858.
Campanea picturata J. D. Smith, Bot. Gaz. (Crawfordsville) 15: 28, *pl. 3*. 1890. TYPE: Guatemala, *Smith 1501* (US, holotype; GH, US, isotypes).
C. oerstedii var. *laevis* Morton, Publ. Field Mus. Nat. Hist., Bot. Ser. 18(4): 1157. 1938. TYPE: La Palma, Prov. San José, Costa Rica, *Maxon 448* (US).
C. chiriquana Morton, Ann. Missouri Bot. Gard. 26: 310. 1939. TYPE: Panamá, *Woodson et al. 935* (US, holotype; MO, isotype).

Robust epiphytic *herbs*, or *shrubs* climbing on large trees by adventitious roots; stems 0.5–3.0 m tall, 0.5–1.0 cm in diam., often woody, terete, green to reddish brown, densely pilose or tomentose with articulated hairs, becoming gray brown and glabrescent with age; branches numerous. *Leaves* toward the ends of the stems and branches; the blades lanceolate, ovate, or oblong, asymmetrical, often falcate, 7.5–22.8 cm long, 4.3–10.6 cm wide, the apex acuminate, the base acute to cuneate and decurrent into the petiole, crenate serrate toward the apex, entire toward the base, the upper surface dark green to reddish brown, tomentose to scabrous, the lower surface lighter green, light brown to reddish, villous with brownish hairs along the veins; petioles subsulcate, 0.3–4.3 cm long, 1–2 mm wide, green to reddish brown, densely villous. *Inflorescences* axillary in upper leaf axils, each usually about twice as long as the subtending

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FIGURE 5. *Capanea grandiflora* (Kunth) Decne. ex Planch.—A. Flowering branch (×⅜). [After *White 62* (MO).]—B. Fruit (×⅗).—C. Seed (×7⅕). [After *Blum & Dwyer 2621* (MO).]

B
C
A
J.E. klein

leaf, cymose; peduncles usually pendent, much elongated, 10–20 cm long, 1–2 mm in diam., green to reddish brown, villous or tomentose; primary bracts leaflike, linear or lanceolate, 1.0–1.5 cm long; pedicels usually less than ⅓ the length of the peduncle, but otherwise similar. *Flowers* showy, large, 1–9 per inflorescence; calyx lobes erect but reflexed in fruit, broadly to narrowly triangular, 6–9 mm long, the apex acute to acuminate, green to reddish brown outside, often reddish at the margin of the lobe, villous, the veins usually obscured by the dense indumentum, the hairs lighter on the inner surface; corolla white, pale yellow, or pale green with red or purple spots inside, 2.5–4.5 cm long, 1–2 cm wide, the tube broadly ventricose to campanulate, slightly constricted above the base, densely villous outside, glandular puberulent inside, the limb of 5 rotund lobes, 0.6–1.0 cm broad, the upper lobes erect to reflexed, the lower lobes spreading, entire; stamens reaching the mouth of corolla tube, the filaments ca. 2 cm long, ca. 2 mm broad at the base and narrowed above, reddish, sparsely pubescent, the anthers yellow, 2–3 mm long, staminode ca. 2 mm long with an undeveloped anther; nectarial glands 5, barely connate at the base, glabrous; ovary ovoid, 4–8 mm broad, green or reddish, the apex villous, the style curved, 2–3 cm long, green or reddish, glandular pubescent, the stigma stomatomorphic. *Fruit* globose to ovoid, surrounded by the persistent calyx, ca. 1 cm in diam., brown, villous; seeds dark brown, linear, twisted, ca. 1 mm long. *Chromosomes* $n = 13$ (Davidse, 1970, based on material from Costa Rica as *Capanea oerstedii*).

Specimens of *Capanea grandiflora* have been collected from Guatemala south to Ecuador and east in northern South America to Venezuela. In Panamá, the species is known from Bocas del Toro and Chiriquí provinces.

Populations of *Capanea grandiflora* from Guatemala, Costa Rica, and Panamá have been distinguished as separate taxa on the basis of the width and venation of the calyx lobes, and in quantity and distribution of the hair covering. These characters are variable over the full range of the species and the expression is probably influenced by the various habitats in which the plants may be found.

BOCAS DEL TORO: Róbalo Trail, N slopes of Cerro Horqueta, 6000–7000 ft, *Allen 5008* (MO). CHIRIQUÍ: Cerro Punta, 2000–2500 m, *Allen 3518* (BM, E, MO, US, US); 7000 ft, *Blaisdell 343* (FSU). Cerro Horqueta, 7000 ft, *Blum & Dwyer 2621* (DUKE, MO, MO, SCZ); *Blum et al. 2412* (F, FSU, MO, SCZ). Las Nubes, 2.7 mi NW of Río Chiriquí Viejo W of Cerro Punta, 2200 m, *Croat 22378* (GH, MO, NY). Above I.D.A.A.N. water tank in Cerro Punta, 700 m, *Croat 26341* (MO), *26349* (MO). E of Boquete on Cerro Azul near Quebrada Jaramillo, 1620–1700 m, *Croat 26859* (MO). Cerro Horqueta, 1650 m, *Croat 26980* (MO). Río Chiriquí Viejo just above Guadalupe, *Croat & Porter 16018* (MO). Above Cerro Punta, 7600 ft, *D'Arcy 5345* (MO). Alto Respinga and above, 2800 m, *D'Arcy 9962* (MO). Pastures and cut over areas just above Bajo Chorro, 1000–2000 m, *D'Arcy 11096* (MO, US). Bajo Chorro, Boquete District, 6000 ft, *Davidson 48* (F, MO, US). Above Boquete, 1650–1800 m, *Dressler & Williams 4005* (DUKE, MO, PMA). Boquete Trail, Cerro Respinga, E of town of Cerro Punta, 2000–2500 m, *Gentry 5924* (MO, NY, PMA). Cerro Horqueta, cloud forest, 6500 ft, *Hagen & Hagen 2088* (NY). Between Pinola and Quebrada Hondo toward summit on Chiriquí Trail, *Kirkbride & Duke 889* (MO). Cerro Punta, *Lindsay 472* (BH, F). Las Nubes, 5 km NW of Cerro Punta, 6000–6500 ft, *Mori & Bolten 7242* (MO). Cerro Pando ca. 16 km NW of El Hato del Volcán, 2000–2483 m, *Mori & Bolten 7265* (MO). Near Paso de Respingo, 2300 m, *Mori & Kallunki 5732* (MO). Cerro Punta, 6800 ft, *Ridgeway & Solís 2401* (GH, MO). Valley of the upper Río Chiriquí Viejo, Monte Lirio, 1300–1900 m, *Seibert 305* (MO). Trail to Alta Respinga above town of Cerra Punta, 2500–2800 m, *Skog et al. 4007* (E, MO, P, PMA,

US). NE of Boquete 5 km, 1700–1800 m, *Skog et al. 4042* (US), *4045* (MO, US). Bajo Chorro near Río Caldera, 1900 m, *Skog & D'Arcy 4100* (MO, US). Boquete, Finca Collins, 5800–6700 ft, *Stern et al. 2051* (MICH, MO, US). Cerro Bambito, 1 mi SW of Cerro Punta, 5600 ft, *Tyson 5680* (FSU, MO, SCZ). 6 mi above Cerro Punta on the Boquete trail, 7500 ft, *Tyson 7162a* (PMA). Approach to Cerro Horqueta, 1940 m, *Utley et al. 277* (DUKE). Río Chiriquí Viejo valley near Monte Lirio, *White 62* (MO, US). Valley of upper Río Chiriquí Viejo, 1300–1900 m, *White & White 20* (MO, US, US). Trail from Bajo Grande along the Quebrada Grande to the top of Paso de Respingo, 2100–2400 m, *Wilbur et al. 15178* (DUKE, MO). Trail between Cerro Punta and the Quebrada Bajo Grande, 2000–2100 m, *Wilbur et al. 11916* (DUKE, MICH, MO). E of Guadalupe along Río Chiriquí Viejo 2 km NE of Cerro Punta, 7000 ft, *Wilbur et al. 13088* (DUKE, F, MICH, MO). Casita Alta, Volcán de Chiriquí, 1500–2000 m, *Woodson et al. 935* (MO, US). Bajo Chorro, 1900 m, *Woodson & Schery 656* (GH, MO, US).

5. CHRYSOTHEMIS

Chrysothemis Decne., Rev. Hort. 21 [sér. 3, 3]: 242. 1849. TYPE: *C. pulchella* (Donn ex Sims) Decne.

Tussacia Benth., London J. Bot. 5: 360, 363. 1846, not *Tussaca* Raf., 1814. TYPE: *T. rupestris* Benth. = *Chrysothemis rupestris* (Benth.) Leeuw.

Terrestrial or epiphytic *herbs* from perennial tubers; stems short lived, weak, succulent with thin watery sap, erect or sometimes decumbent, subquadrangular, green, pubescent with transparent few celled glandular or eglandular trichomes. *Leaves* opposite, equal or subequal in a pair, membranous, lanceolate, elliptic, ovate, or oblanceolate, dentate or crenate, usually dark green and sparsely pubescent with broad-based trichomes above, light green or purplish to roseate and pubescent especially along the prominent veins beneath, the lateral veins 7–8, arching toward the apex; petioles short, usually decurrent with the blade, green, pubescent. *Inflorescences* numerous, pedunculate, axillary but appearing terminal by exceeding the stem apex, cymose or umbellate, ⅛–½ the length of the subtending leaf; bracts small, leafy; peduncles and the pedicels slender, terete, green or reddish, pubescent. *Flowers* somewhat zygomorphic, 1–9 per peduncle; calyx of 5 connate sepals, winged or not, inflated or campanulate to urceolate, subcordate or rounded at the base, yellow green, orange or red; corolla of 5 connate petals erect in the calyx, with a flaring 5-lobed limb, yellow to orange with orange or reddish lines, the tube cylindric, not spurred but gibbous, glabrous or pubescent externally, internally with a ring of hairs at the stamen insertion and glandular hairs above, the mouth oblique, the lobes of the limb rounded to orbicular, nearly entire; stamens 4, the staminode lacking, didynamous, included, the filaments slender, flattened, glabrous, basally connate and inserted briefly on the corolla base, the anthers orbicular, 1–2 mm in diam., sometimes coherent, dehiscent by longitudinal slits, connective thickened; nectary posterior, bilobed or rarely to four separate glands; ovary superior, spheric, conic, or ovoid, pilose, style usually glabrescent, the stigma bilobed, glandular, the ovules numerous on the inner surface of the placental lamellae. *Fruit* a fleshy capsule included in the persistent calyx, globose to ovoid, bivalved, glabrescent; seeds dark brown, obliquely striate, ellipsoidal or rhombic, shiny, the base mucronate, often with a remnant of white funiculus, the embryo straight.

Chrysothemis is a genus of 6 species in the West Indies, Central and northern

South America growing at low elevations. The pollinators of *Chrysothemis* are not known for certain, but euglossine bees are suspected. Ants are possibly responsible for seed dispersal, attracted by the fleshy funiculi.

Plants of the Panamanian species are sometimes grown as garden or greenhouse subjects; the orange or red persistent calyces are considered attractive.

Literature:

Leeuwenberg, A. J. M. 1958. Revision of *Chrysothemis* (*Tussacia*). Acta Bot. Neerl. 7: 329–340.

Moore, H. E., Jr. 1954. *Chrysothemis* and *Tussacia*. Baileya 2: 86–88.

a. Calyx green to pale yellow, inflated, subcordate at the base; peduncles usually equalling or shorter than the pedicels; corolla usually glabrous ..... 1. *C. friedrichsthaliana*

aa. Calyx deep orange to red, not inflated, rounded at the base; peduncles usually longer than the pedicels; corolla pilose, at least at the base of the lobes ..... 2. *C. pulchella*

1. **Chrysothemis friedrichsthaliana** (Hanst.) H. E. Moore, Baileya 2: 87. 1954.

Tussacia friedrichsthaliana Hanst., Linnaea 34: 337. 1865. TYPE: Guatemala, *Friedrichsthal 1252* (W, not seen; photo MO, US).

Weak, terrestrial or rarely epiphytic *herb*, to 60 cm tall; stem erect or trailing, green, pilose especially toward the apex, 2–7 mm in diameter, the nodes thicker; tuber 1–3 cm in diam., with one or more shoots. *Leaves* with blades lanceolate, elliptic, ovate or oblanceolate, 7.5–37.5 cm long, 2.5–13.5 cm wide, the apex acute to acuminate, the base long decurrent into the petiole, occasionally oblique, crenate to dentate, the upper surface dark green, sparsely pilose, the lower surface light green to purple and pilose along the veins; petioles flattened, to 1 cm long, green, pilose. *Inflorescences* axillary, showy, of single flowers or of up to 9 flowers in compound cymes or umbels; peduncles slender, terete, usually equalling or shorter than the pedicels, rarely to 4 cm long, green, puberulent; bracts leaflike, linear to lanceolate, to 1.5 cm long and 3 mm wide, green to purple, pilose on both sides; pedicels to 3 cm long, green, pilose. *Flowers* with sepals fused into an inflated cuplike, winged and 5-angled calyx, inflated, subcordate at the base, the tube 0.6–1.5 cm long, ca. 1 cm in diam., green to yellow, sparsely pilose outside, puberulent to glabrous inside, the lobes deltoid, 2–5 mm long, acuminate, dentate to erose, corolla greenish yellow to orange or salmon red with reddish longitudinal lines, "nectar-guides," out to the limb, the tube 1.4–2.7 cm long, 5–8 mm wide at the middle from a constriction above the base, flaring to 1.2–2.0 cm at the limb, outside usually glabrous, occasionally sparsely pilose at the base of the limb, inside glabrous but for glands at the mouth of the tube, the limb suboblique, the lobes porrect, 4–7 mm broad, orbicular, subentire, glandular; stamens inserted at the base of the corolla tube, not exserted, the filaments coiling or recurved at the apex after dehiscence, the anthers oblong, ca. 1 mm long, often coherent in a square; nectary yellow, bilobed or entire, rarely several lobed; ovary superior, pilose, the style to 1.5 cm long, rarely pubescent. *Fruit* a fleshy capsule surrounded by the persistent calyx, globose, bivalved, 7–10 mm in diam.; seeds dark brown, shiny, with

prominent oblique ridges, ca. 0.6 mm long, 0.3 mm in diameter, funiculus translucent, fleshy.

Chrysothemis friedrichsthaliana ranges from Nicaragua south to Ecuador. In Panamá the species is found below 200 m in shaded wet forests and moist openings and is reported by Allen (*4594*) to be common in banana plantations in Darién. The type, *Friedrichsthal 1252*, was believed by earlier authors to have come from Guatemala, but according to Gibson (1974) the species has never been recollected in Guatemala. Also, she reports that Friedrichstal's "Guatemalan" plants are known now to have been collected in Costa Rica and Panamá.

This species is used by the Indians as a folk remedy according to information available with specimens collected by Duke in Darién and Panamá. In the province of Panamá, the plant is known as "Wilkwa" and used by the Cuna Indians in the treatment of snakebite. In Darién, *C. friedrichsthaliana* is known by two different names. Under the name "Ceodotaona," the plant is used to reduce swelling and black eyes. Under the Spanish name "Debaratodor," the Chocó Indians use the plant for curing diarrhea and snakebite.

BOCAS DEL TORO: Region of Almirante, Research Lagoon, *Cooper 142* (F, NY). Changuinola Valley, *Dunlap 352* (F, US). 10–15 mi inland S from mouth of Changuinola River, *Lewis et al. 865* (MO, US). Chiriquicito to 5 mi S along Río Guarumo, *Lewis et al. 2030* (MO, MO, REED, US). Water Valley, *Wedel 789, 1458* (both MO, US). Chiriquí Lagoon, *Wedel 1130* (MO). Little Bocas, Chiriquí Lagoon, *Wedel 2509* (MO, US). Darkland, Chiriquí Lagoon, *Wedel 2621* (MO, US). CANAL ZONE: Barro Colorado Island, *Aviles 33* (F); *Bailey & Bailey 20* (BH, F); *Bangham 600* (F); *Croat 4177* (MO), *5930* (MO, SCZ), *5979* (F, MO, SCZ), *6414, 11708* (both MO); *Ebinger 16* (F, MICH, MO, US); *Kenoyer 536* (US); *Killip 40038* (US); *Knight 69-90* (MO); *Luteyn 764* (DUKE); *McDaniel 5016* (FSU, MO); *Shattuck 62, 78* (both F, MO); *Standley 40952* (BM, US), *41121* (US); *Starry 158* (MO), *180* (MO, SCZ); *Woodworth & Vestal 403* (F). Azote Caballo road, near Madden Dam, 100 m, *Allen 2674* (MO, US). Juan Mina, hill at Canal Zone boundary, *Bartlett & Lasser 16571* (MICH). Juan Mina, *Bartlett & Lasser 16713* (MICH). Road S-11, NW of Escobal, *Croat 12452* (MO, SCZ). Pipeline Road within 5 mi of Gamboa Gate, *D'Arcy 9282* (MO, US). Woods near Marine Grounds near Rodman, *Dwyer 2723* (MO). *Epplesheimer* 1910 (F). Road to Boy Scout Camp off Madden Dam Road, *Kirkbride 56* (F, MO, NY). Summit Gardens, 0–100 m, *Mori & Kallunki 1883* (MO). Pipeline Road, *Mori & Kallunki 2052* (MO). Madden Dam near Río Chagres, 50–75 m, *Seibert 556* (MO, NY, US). Las Cruces, 26–40 m, *Seibert 569* (MO, US). Upper Chilibre River ½ to 1 mi below Chilibre, *Seibert 1507* (US). Chiva Chiva Trail near Miraflores Lake, *Tyson 1401* (FSU, MO, SCZ). Salamanca Hydrographic Station, Río Pequeni, 80 m, *Woodson et al. 1614* (MO, NA, NY, US). Pipeline Road, *Witherspoon & Witherspoon 8307* (MO). Madden Lake beyond dam, *Witherspoon & Witherspoon 8793* (MO, US). CHIRIQUÍ: San Bartolo Arriba W of Puerto Armuelles, 125 m, *Croat 26706* (MO). San Bartolomé, Peninsula de Burica, 0–50 m, *Woodson & Schery 878* (MO, NY, US). COLÓN: Río Guanche ca. 3–5 mi inland, 10–100 m, *Croat 26212* (MO). Río Guanche, *D'Arcy 9716* (MO). Disturbed forest on steep hill behind Portobelo, *Croat & Porter 15602* (MO, NY). Río Guanche, 1–4 km upstream from Portobelo Road, 0–100 m, *Gentry 8765* (MO). Road to Mosquera from Palmas Bellas nearer Mosquera, *Mori & Kallunki 1961* (MO). Forests around Portobelo, 5–100 m, *Pittier 2488* (US). Loma de la Gloria, near Fató, 10–104 m, *Pittier 4085* (US). DARIÉN: Headwaters Río Chico, 500–750 ft, *Allen 4594* (MO, US). Gold mine at Caná, 500–600 m, *Croat 37596* (MO). Santa Fé, Río Sabana, 1–3 mi SE on Panamerican Highway, *Duke 4108* (MO). Road from El Real to Pinogana, *Duke 4886* (MO). Ca. 10 mi S of El Real on Río Pirre path from Pucro to Río Pucro, *Duke 5359* (MO). 10 mi S of El Real on Río Pirre, *Duke 5466* (MO). Without locality, *Duke 8195* (MO). Loma Cuasí behind Manené, *Duke 13629* (MO). Tumaganti, 300 m, *Duke 14153* (F, MO, NY). Interamerican highway, ca. 1 mi SE of Río Tuira, *Duke 14547* (MO, REED). Río Balsa between Manené and Guayabo, *Duke & Nickerson 14957* (MO). Choco village, Piji Vasal sea level, *Folsom 4556* (MO, US). Río Tuquesa at middle Tuquesa Mining Company camp called Charco Peje, 250 m, *Mori 7007* (MO). Paya, *Stern et al. 187A* (MO, US). Peñas Bay near hotel,

Tyson 5541 (FSU). Periaque camp at river, *Tyson et al. 4750* (FSU, MO, REED, SCZ). Caná, 2500 ft, *Williams 939* (NY, NY). PANAMÁ: Panamerican Highway, open grazed area near Jenené, Río Camita, *Duke 3825* (MO, PMA). El Llano, *Duke 5524* (MO). Near confluence of Río Pacora and Río Corso, 450 m, *Duke 11960* (MO, NY, OS). Piría-Cañasas trail near Piría, 100 m, *Duke 14327* (MO, OS). Between Cañasas and Sabalo, 100 m, *Duke 14487* (MO). San José Island, valley below main camp, *Erlanson 493* (MICH, MO, NA, NY). San José Island, near South Road, *Erlanson 574* (US). Forest from first sharp bend on Río Pasiga, 0–2.5 mi along lumber road to Río Maestro, *Gentry 2329* (MO). San José Island, East Road, *Harlow 34* (US); *Johnston 141* (US). Tributary or Río Chagres, 5 mi SW of Cerro Brewster, 1000 ft, *Lewis et al. 3409* (MO). Capira, *Paul 134* (US). Forests on dry limestone around Alhajuela, Chagres Valley, 30–100 m, *Pittier 3490* (US). Between Pacora and Chepo, 25 m, *Woodson et al. 1642* (MO, NA, NY, US). SAN BLAS: Headwaters of Río Mulatupo, *Elias 1740* (MO). Permé, *Cooper 258* (NY[p.p.]). Coastal plain, Niatuppu, *Stier 208* (MO). WITHOUT LOCALITY: *Bristan 204* (NY).

2. **Chrysothemis pulchella** (Donn ex Sims) Decne.,[8] Rev. Hort. 21 [sér. 3, 3]: 242. 1849.—FIG. 6.

Besleria pulchella Donn ex Sims, Bot. Mag. 28: *tab. 1146.* 1808. TYPE: Cultivated, Springwell, Hertfordshire, England, *Woodford* (BM, not seen).
Tussacia pulchella (Donn ex Sims) Reichenb. ex Oerst., Cent. Gesn. 39. 1858.
T. woodsonii Morton, Ann. Missouri Bot. Gard. 26: 308. 1939. TYPE: Panama, *Woodson et al. 1195* (US, holotype; MO, NY, US, isotypes).

Terrestrial or rarely epiphytic *herbs*, to 90 cm tall; stems erect when young, decumbent with age, rarely branched, freely producing adventitious roots at the nodes, terete at the base, subquadrangular above, green or purplish, densely pilose toward the apex, glabrescent below, slender, 5–12 mm in diam. but with thicker nodes; tuber brown, spheroidal, 2–3 cm in diam. with one or more shoots. *Leaves* with blades lanceolate, elliptic to ovate, 9–30 cm long, 3–12 cm wide, the apex acute, the base long decurrent into the petiole, crenate or dentate, above dark green, shining, subbullate, sparsely pilose to subscabrous, below lighter green to pink purple along the veins or generally, pilose; petioles less than 1 cm long, 1–2 mm broad, green, pilose. *Inflorescences* erect, umbellate, of 3–9 flowers; peduncles solitary in each axil, usually longer than the pedicels, 1.6–2.8 cm or more long, green or red, pilose, bearing at the apex 2 linear lanceolate leaflike bracts, 4–15 mm long, 1–6 mm wide, pilose; pedicels green or red, pilose, 1.0–2.5 cm long. *Flowers* red orange and yellow; calyx tubular campanulate, 5-angled or winged, not inflated, the base rounded, the tube 1.0–1.8 cm long, 0.5–1.1 cm wide, orange to red, pilose to villous outside, glabrous or rarely pubescent inside, the lobes small, broadly triangular, 2.5–5.0 mm long, ca. 3.5–5.0 mm broad at base, abruptly acuminate with a glandular denticulate margin; corolla orange or yellow with reddish orange stripes in the tube extending out to the limb, 1.6–3.0 cm long, exceeding the calyx about 2 times, the tube gibbous and 3–6 mm wide at the base then slightly constricted but broadening to 6–8 mm below the limb, outside glabrous near base but densely pilose with white trichomes above, 2 longitudinal ridges extending down the tube, inside glandular pubescent, the limb patent to erect, the lobes suborbicular, subequal, ca. 4 mm long, 7–8 mm broad, entire; stamens 4, attached to the base of the corolla tube, the filaments whitish, glabrous, ca. 10–11 mm long or about ¾

[8] Additional synonyms are listed by Leeuwenberg (1958). Only those names used for Panamanian material have been included here.

FIGURE 6. *Chrysothemis pulchella* (Donn ex Sims) Decne. Habit (×½). [After *Oliver et al.* 3568 (MO).]

the length of the corolla tube, somewhat curved, the anthers coherent or free, oblong, 1–2 mm long, ca. 0.75–1.8 mm wide, the connective thick, glabrous; disc gland yellow or green, ca. 1.5 mm long and wide, bilobed or entire; ovary conic, superior, pilose, the style thick, straight, shorter than the filaments, glabrous, the stigma deeply bilobed. *Fruit* a fleshy pubescent capsule surrounded by the persistent calyx, ovoid, glabrescent, ca. 6 mm in diam.; seeds dark brown, ellipsoidal or rhombic with prominent diagonal striations, ca. 0.5 mm long, the funiculus whitish. *Chromosomes* $n = 9$ (Taxon 20: 351).

This species is more widespread than *Chrysothemis friedrichsthaliana*. However, *C. pulchella* is not found north of Panamá in Central America. Its habitat is usually damp forests on wet rocks at low elevations in Panamá and the West

Indies, and in northern South America from Surinam to western Colombia and Brazil.

BOCAS DEL TORO: Isla Colón, 0–120 m, *Wedel 492* (MO). CANAL ZONE: Summit Garden, Palm Grove, *Croat 11057* (MO, NY, USF). Madden Dam, *Hayden 79* (MO). 5 mi N of junction of the Interamerican Highway and on C-10 artillery road, *Lazor 5458* (MO), *5459* (NA). Curundu, Survival School area, *Tyson 1306* (FSU, MO, SCZ). CHIRIQUÍ: San Félix, 100 m, *Allen 3652* (F, MO, US). Tolé vicinity of Santa Ana Well, 1000 ft, *Dwyer & Kirkbride 7458* (MO, US). San Félix, 0–120 m, *Pittier 5200* (US). David, *Roy 3* (US). Tolé, *Tyson et al. 4228* (FSU, MO, SCZ). Río Chiriquí to Remedios, 15–50 m, *Woodson et al. 1195* (MO, NY, US, US). COLÓN: Río Boquerón, 6–8 km upstream from Peluca Hydrographic Station, *Dressler 4700* (PMA). DARIÉN: 10 mi S of El Real on Río Pirre path from Pucro to Río Pucro, *Duke 5360* (MO, NY). Cultivated, El Real, *Stern et al. 967* (MO). LOS SANTOS: From 1 mi S to 10 mi N of Tonosí, *Duke 12485* (MO, US). Los Toretos, *Dwyer 2453* (MO, US). Woods N of village of Guaniquito, ca. 10 mi N of Tonosí along Río Tonosí, 100–200 m, *Luteyn & Foster 1369* (DUKE). Road between Tonosí and Macaranas, *Oliver et al. 3568* (MO, SCZ). PANAMÁ: Near abandoned house in rocks, Tocumen, *Dwyer 4371B* (MO). Tocumen Airport, *Dwyer 4394A* (MO). Cerro Campana, 8.6 mi SW of Capira, 700 m, *Luteyn 989* (DUKE). SAN BLAS: Permé, *Cooper 258* (F, US—specimen at NY is *C. friedrichsthaliana*). VERAGUAS: Coiba Island, *Collenette 465* (US). Río Trinidad, *Dwyer 1326* (MO, MO). Isla de Coiba, *Dwyer 2356* (F, NY, SCZ). 50 km E of Santiago, *Folsom 3923* (MO, US). Uva valley of the Contreras Islands, *Foster 1586* (DUKE, F, NY, PMA). Between Tolé and Santiago, 50 mi from Santiago, *Kirkbride & Hayden 174* (MO, MO, NY, SCZ). Isla de Uva, Contreras group, *Pittier 5111* (US). Road between Santiago and David, *Stern et al. 1000* (MO, US). WITHOUT LOCALITY: Panamá, collector unknown, *Bernhardi Herbarium* (MO). Panamá, *Hayes 759* (NY).

6. CODONANTHE

Codonanthe (Mart.) Hanst., Linnaea 26: 209. 1854, nom. cons., not *Codonanthus* G. Don (1838—Loganiacene)

Hypocyrta sect. *Codonanthe* Mart., Nov. Gen. 3: 1829. TYPE: *Hypocyrta gracilis* Mart. = *Codonanthe gracilis* (Mart.) Hanst.

Coccanthera C. Koch & Hanst., Ind. Sem. Hort. Reg. Bot. Berol. 1855: App. 17. 1855. TYPE: *C. devosiana* (Lem.) C. Koch & Hanst. = *Codonanthe devosiana* Lem.

Codonanthopsis Mansf., Repert. Spec. Nov. Regni Veg. 36: 120. 1934. TYPE: *C. ulei* Mansf. = *Codonanthe ulei* (Mansf.) H. E. Moore.

Epiphytic *shrubs* or *lianas* or *herbs*, usually growing on ants' nests; branches few, stems pendent, repent, or erect, to 2 m tall, becoming woody; adventitious roots and/or extrafloral nectaries sometimes produced from the nodes. *Leaves* opposite, equal to rarely strongly unequal in a pair; blades fleshy, becoming coriaceous when dry, entire, sinuate or serrulate toward the apex, often with reddish extrafloral nectaries on the lower surface; petioles usually short. *Inflorescences* of one or few flowers in the upper leaf axils; peduncles, if present, very short; bracts lacking; pedicels short. *Flowers* with the calyx 5-lobed or bilabiate, when 5-lobed the lobes nearly equal to very unequal, the dorsal lobe often recurved; corolla white, pink, lilac, yellow, or deep purplish, often with reddish lines or spots, oblique in the calyx, the tube funnelform to subcampanulate, the base spurred or rounded, gradually or abruptly broader toward the throat, or somewhat compressed or grooved, the limb spreading, of 5 rounded lobes; stamens 4, inserted at the base of the corolla tube, included, the filaments adnate to the base of the corolla tube, briefly connate at the base, recoiled or lowered after pollen shed, the anthers laterally oblong, coherent in pairs by tips or sides, later separating, dehiscing by pores; disc a single dorsal nectary, usually

large; ovary superior with 2 parietal placentas ovuliferous on the inner side, the style included but elongating after pollen shed, the stigma bilobed to stomatomorphic. *Fruit* a fleshy berrylike capsule, tardily dehiscent or dehiscing by 2 valves, globose, ovoid, or compressed, red, pink, orange, or yellow green; seeds colored red, pink, or yellow, fusiform or ellipsoid, obliquely striate, the funicle often fleshy or the seed surrounded by an aril. *Chromosomes* $n = 8$ or 16 (Wiehler, 1975b).

Codonanthe is a genus of about 15 species that occurs from México to Brazil, and from the Lesser Antilles to Peru and Bolivia.

Several species are in cultivation as house or greenhouse plants where they tolerate the less moist and warm conditions than are available in their usual wild habitats in moist forests.

Plants are usually associated with ants in various ways. The plants seem to be epiphytic on nests of ants, and the plants often have extrafloral nectaries on the undersides of the leaves, between the bases of the calyx lobes, or at the nodes. The colored seeds are covered by a gelatinous aril or have a funicle that may be associated with ant dispersal.

The name *Codonanthe* was probably chosen by Martius to refer to the subcampanulate corolla in some of the species.

Literature:

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———. 1975b. *Codonanthe luteola* (Gesneriaceae), a new species from Panama. Selbyana 1: 157–164.

———. 1977. Cultivated species of *Codonanthe*. The Gloxinian 27(1): 5–7.

a. Anther sacs bearing two horns near the pore; calyx lobes with prominent raised midvein; leaves oblanceolate, less often elliptic or obovate in outline, margin prominently toothed and usually sparsely dentate, seldom entire; stems erect at least at the tips; fruiting pedicels curved in fruit ..... 5. *C. uleana*

aa. Anther sacs lacking horns; calyx lobes flat or curved without raised midvein; leaves of various outline, usually not oblanceolate, margin almost always entire or sinuate toward the apex; stems repent or pendent, ascending only in *C. chiricana*; fruiting pedicels not noticeably curved.

b. Corolla tube white with a red area inside throat, or if red area not obvious then tube arcuate, 2.0–3.5 cm long, 2 prominent ridges on the inner lower side; capsule ovoid and acute to acuminate, dehiscing by 2 recurving valves ..... 4. *C. macradenia*

bb. Corolla tube yellowish or white, but without the red area within near throat, tube straight on dorsal side, usually smaller or larger than *C. macradenia*, lacking ridges within; capsule tardily dehiscent and subglobose, or condition at dehiscence unknown.

c. Stems ascending; spur spotted red, corolla tube ca. 3.5 cm long .. 1. *C. chiricana*
cc. Stems pendent or repent; spur not reddish unless tube of corolla more than 3.5 cm long.
d. Corolla white, with or without a pink flush on lobes, yellow on lower inner surface, tube 1.2–1.8 cm long; calyx lobes puberlous ..... 2. *C. crassifolia*
dd. Corolla yellowish throughout, except spur reddish, tube more than 3.6 cm long; calyx lobes hirsute ..... 3. *C. luteola*

1. **Codonanthe chiricana** Wiehl., Selbyana 2: 95, *pl.* 28*C*. 1977. TYPE: Cultivated at Marie Selby Botanical Gardens from plants collected in Prov. Chiriquí, Panamá, *Wiehler 77110* (SEL, holotype, not available for study).

Epiphytic *herbs*; stems erect or ascending, to 15 cm long, 3–5 mm in diam., reddish when young, becoming gray with age; branches numerous. *Leaves* decussate, equal in a pair, broadly ovate, 0.5–1.2 cm long, succulent, the apex acute, the base decurrent, subentire to crenulate, above and below green with reddish margins, glabrous to sparsely pubescent; petioles 0.5–1.2 cm long. *Inflorescences* axillary, of single flowers; peduncles lacking; bracts ca. 1 mm long; pedicels 3–4 mm long, red, pubescent. *Flowers* showy; calyx lobes nearly equal, lanceolate, 5–7 mm long, thick, green with reddish apices, pubescent; corolla white with a reddish spur, the tube oblique in the calyx, ca. 3.5 cm long, constricted above the spur, then expanded to ca. 1 cm wide near the limb, the outside pubescent, the inside glandular, the lobes of the limb patent or spreading, nearly equal, 0.9–1.1 cm long, erose; stamens included, the filaments 2.0–2.2 cm long, adnate to the base of the corolla tube, glabrous below, pilose above, the anthers in 2 pairs, 2 mm long, white, dehiscing by a central pore, lacking hornlike projections; disc of 4 connate glands and 1 distinct anterior gland, each white, glabrous; ovary pubescent, the style ca. 2.1 cm long, white, pilose, stigma stomatomorphic. *Fruit* fleshy, 1.6 cm long, red, pubescent; seeds fusiform, ca. 3 mm long, striate, red.

As no specimens of this species have been seen, the description is adapted from the original.

Codonanthe chiricana is apparently distinctive by its erect or ascending, but compact habit, and by its large white corolla with reddish spur. The type clone was collected in Panamá in the province of Chiriquí from near Valle Hornito and Cerro Hornito at the site of Fortuna Dam, 1,000–1,400 m elevation.

2. **Codonanthe crassifolia** (Focke) Morton, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1159. 1938.

Hypocyrta crassifolia Focke, Tijdschr. Wis-Natuurk. Wetensch. Eerste Kl. Kon. Ned. Inst. Wetensch. 5: 199. 1852. TYPE: Surinam, *Focke*, colored drawing (L; US, photo).
Codonanthe confusa Sandwith, Bull. Misc. Inform. 1931: 492. 1931. TYPE: Karouany, French Guiana, *Sagot 426* (K, holotype; P, isotype, US, photo).
C. formicarum Fritsch, Bot. Jahrb. Syst. 37: 491. 1906. TYPE: Río Juruá, *Ule 5776* (B, holotype probably not extant).
Episcia hookeri Hanst., Linnaea 34: 350. 1865. TYPE: Trinidad, *Purdie* (not seen).

Epiphytic *subshrubs*; stems pendent, repent, or creeping, usually ca. 30 cm long, occasionally to 2 m, 2–4 mm in diam., the nodes larger, green to reddish,

the apex puberulent, glabrous below. *Leaves* nearly equal in a pair; blades elliptic to oblong or ovate, 1.5–5.5 cm long, 0.8–2.2 cm wide, fleshy or succulent, the apex acute, rounded to cuneate at the base, nearly entire, above dark green, rarely reddish, glabrous to minutely puberulent, below lighter green or reddish, the midvein often prominent; petiole rarely more than 1 cm long, puberulent, red extrafloral nectaries sometimes at the bases. *Inflorescences* axillary, 1 or 2 flowered; pedicels ca. 5 mm long, puberulent. *Flowers* small, uncommon, the calyx lobes free, nearly equal, the posterior lobe forced back by the corolla spur, each linear lanceolate, 2–9 mm long, green or reddish, puberulous, with reddish nectaries at the sinuses of the lobes; corolla white or cream colored, yellow on lower surface inside, rarely pink on the lobes, the tube oblique in the calyx, spurred at the base, less than 2 cm long, 1–2 mm wide at base, broader above, 5–8 mm wide at the throat, glabrous or puberulent outside, glandular inside, not grooved or ridged, limb lobes spreading, rotund, 2–6 mm wide, nearly entire; stamens included, the filaments ca. 8 mm long, adnate to the base of the corolla, glabrous or minutely glandular puberulent, the anthers rounded, ca. 1 mm long, yellow, coherent in pairs, connective angled; disc gland solitary, glabrous; ovary puberulous, style ca. 10 mm long, glabrate, the stigma stomatomorphic. *Capsule* tardily dehiscent, subglobose, ca. 1 cm in diam., pink to red, shiny, puberulent to glabrescent, the apex not prominent; seeds enclosed in the aril, oblong, ca. 2 mm long, longitudinally striate, reddish to brown. *Chromosomes* $n = 16$ (Wiehler, 1975b).

As Moore (1973) wrote, "*Codonanthe crassifolia* has the greatest range and the most variable morphology of any species in the genus." The species is distributed through Central America into northern South America south to Peru and Brazil, and east to Venezuela and Trinidad. In Panamá, *C. crassifolia* has been collected most often in the provinces of Bocas del Toro and Darién, and on Barro Colorado Island in the Canal Zone. Its range overlaps somewhat the other species of *Codonanthe* in Panamá. Because of its variable morphology, sterile specimens or those without mature flowers or fruits cannot be identified with certainty. The flowers are smaller than those of any other species in Panamá; the subglobose fruits distinguish this species from the ovoid acute to acuminate fruits of *C. macradenia*. Doubtfully identified specimens are not included in the list below.

BOCAS DEL TORO: Changuinola, *Croat & Porter 16313* (MO). Potrero, Chinguinola valley, *Dunlap 503* (F, US). Almirante, just N of Dos Milla, low swampy area, *McDaniel 5133* (FSU, MO). Chiriquí Lagoon, *Wedel 1156* (MO), *1296* (MO). Old Bank Island, Chiriquí Lagoon, *Wedel 1875* (MO, US). Little Bocas, Chiriquí Lagoon, *Wedel 2549* (MO). Western River, Chiriquí Lagoon, *Wedel 2782* (MO, US). Bastimentos, Mariano Creek, Chiriquí Lagoon, *Wedel 2893* (MO). CANAL ZONE: Barro Colorado Island, *Croat 5423* (MO), *6147* (MO), *8467* (MO); *Foster 1019* (DUKE, F, PMA). Chagres, *Fendler 178* (NY). COCLÉ: Above Penonomé, *Williams 432* (NY). DARIÉN: Alconorque swamp on Río Tuira, ca. 3 mi NW of El Real, *Duke 4816* (MO). Río Pirre, 1–5 mi downstream from El Real, *Duke 4937* (MICH, MO). 1–4 mi N of Pucro, *Duke 13016* (MO). Río Balsa between Manené and Tusijuanda, *Duke 13566* (MO). Río Mortí, Drill Site 7, 250 m, *Duke 14206* (MO, NY). Manené to mouth of Río Cuasí, *Kirkbride & Bristan 1423* (MO, NY). S of El Real, Don Pablo Othon's pasture, foothills of Cerro Pirre, *Stern et al. 760* (MO, US). PANAMÁ: El Llano-Cartí road 11 km from El Llano and junction with Panamerican Highway, 500 m, *Skog & Folsom*

4169 (US). VERAGUAS: Guabal, Río Dos Bocas 16 km NE of Santa Fé, 500 m, *Dressler 4802* (PMA).

3. **Codonanthe luteola** Wiehl., Selbyana 1: 159. 1975. TYPE: Panamá, *Wiehler & Dressler 71184* (US, holotype; BH, MO, isotypes).

Epiphytic vinelike *herbs*; stems slender, repent or pendent, to 1 mm long, 1–3 mm in diam., the nodes thicker and producing adventitious roots, young stems reddish becoming brown to grey, hirsute; branches occasional. *Leaves* decussate, nearly equal in a pair, obovate to suborbicular, 1.2–3.5 cm long, 0.8–2.2 cm wide, succulent, the apex obtuse to rounded, the base cuneate to acute or obtuse, above dark green, glabrous, below lighter green, occasionally pinkish, glandular puberulent especially on the prominent midvein and the margin; petioles 5–10 mm long, usually reddish, pubescent to hirsute. *Inflorescences* axillary, usually of a single flower; peduncles lacking; bracts minute; pedicels ca. 5 mm long or slightly longer, green or reddish, pubescent. *Flowers* showy; calyx lobes unequal, the posterior lobes slightly shorter and bent back by the corolla spur, linear lanceolate, 5–11 mm long, 1–2 mm wide, light green to reddish, puberulent, the veins not prominent; corolla light to cream yellow, spur all reddish or red spotted, the tube horizontal in the calyx, nearly straight, more than 3.6 cm long at anthesis, the spur 2–4 mm long, obtuse, the tube narrowed to ca. 3 mm wide at the apex of the calyx lobes, then somewhat venticose and broader toward the limb, 7–10 mm broad at the throat, sparsely puberulent, the limb oblique, to ca. 1.8 cm wide, the lobes suborbiculate, 4–7 cm wide, the margin subentire; stamens included, the filaments 2.0–2.6 cm long, the anther connective broad, lacking hornlike projections; disc reduced to a single bilobed gland or 2 connate glands, ca. 2 mm long, white or reddish, glabrous; ovary puberulent, the style as long as the stamens, pilose, the stigma stomatomorphic. *Fruits* and seeds not seen. *Chromosomes* $n = 8$ or 16 (Wiehler, 1975b).

Codonanthe luteola is endemic to the province of Panamá occurring at 200–800 m with stems pendent from the larger trees or scrambling on the fallen trunks. The species is distinctive by the long white corolla tube, often over 4 cm long with a reddish spur, and by the spathulate leaves.

PANAMÁ: Newly cut road from El Llano to Cartí-Tupile, 12 mi above Panamerican Highway, 200–500 m, *Croat* 22859 (MO). El Llano-Cartí highway, ca. 20 km N of El Llano, *Dressler* 4633 (DUKE, PMA). Primary forest, Campo Tres, 3 mi NE of Altos de Pacora, 500–800 m, *Liesner* 579 (MO). El Llano-Cartí road, 10–18 km from Panamerican Highway, 350 m, *Mori et al. 4561* (MO); *Nee 10458, 10526* (both MO); *Nee & Tyson 11005* (MO). Cerro Jefe ca. 20 km N of Tocumen airport, 800 m, *Wiehler & Dressler 71184* (BH, MO, US).

4. **Codonanthe macradenia** J. D. Smith, Bot. Gaz. (Crawfordsville) 25: 154. 1898. LECTOTYPE: Borders of the river at Boruca, Costa Rica, *Tonduz 6769* (US, designated by Moore, 1973).—FIG. 7.

Epiphytic vinelike *herbs* or *subshrubs*; stems repent, pendent or creeping, to 0.5 m or more long, to 5 mm in diam., the nodes thicker and producing adventitious roots, green to reddish, puberulent. *Leaves* nearly equal in a pair, ovate,

FIGURE 7. *Codonanthe macradenia* J. D. Sm. Habit (×1). [After *Skog & Butcher 4105* (US).]

elliptic or lanceolate, 1.5–4.0 cm long, 1–2 cm wide, fleshy, the apex more or less rounded acute, the base obtuse to acute, entire to serrulate toward the apex, above and below green, occasionally flushed with pink, puberulous, with reddish extrafloral nectaries below; petioles 1–5 mm long, puberulent. *Inflorescences* axillary, of 1–2 flowers; peduncles absent; pedicels 2–7 mm long, puberulent. *Flowers* with the calyx oblique, the lobes more or less equal, the posterior gland pushed back around the corolla spur, the calyx lobes lanceolate, 4–9 mm long, 0.5–2 mm wide at the base, the apex acuminate attenuate, green or reddish, at least at the tips, puberulous, red glands at the sinuses; corolla cream yellow to white with a reddish area inside, the tube oblique in the calyx with a prominent rounded spur, 2–5 mm long at the base, somewhat curved downward at the rear, the tube arcuate or curved above, 2.0–3.5 cm long, narrowed above the spur, 2–3 mm wide, ampliate above the curve, 6–9 mm wide at the throat, the outside puberulous, the inside glandular, grooved on the lower side, the limb 1.2–1.5 cm wide, the lobes orbiculate, erect or spreading, 4–6 mm long, 5–7 mm wide; stamens included, the filaments ca. 1.5 cm long, white and glabrous below, yellowish and pubescent above, rarely reddish spotted, the anthers coherent or free, oblong, ca. 2 mm long, pores not horned; disc gland posterior, oblong, ca. 2 mm long, shallowly notched; ovary puberulent, the style curved, ca. 1 cm long, pilose, the stigma stomatomorphic to bilobed. *Capsule* ovoid, apiculate, 1.0–1.7 cm long, 8–10 mm in diam., red purple, puberulent, dehiscing by 2 recurving valves; seeds oblong, reddish, 2–3 mm long, surrounded by whitish aril. *Chromosomes* $n = 16$ (Fussell, 1958, as *C. crassifolia*; Wiehler, 1975b).

Codonanthe macradenia is nearly impossible to distinguish from *C. crassifolia* in a sterile condition, but the longer, curved, grooved corollas with an inner reddish patch, and the ovoid, acute to apiculate fruit identifies this species. The range of *C. macradenia* includes the provinces Chiriquí, Colón, Panamá, San Blas, Veraguas, as well as the Canal Zone, but it was originally described from Costa Rica.

CANAL ZONE: San Pablo, Colón to Empire, Panama Railroad, *Crawford* 533 (NY, PH), 563 (PH). Sabanas along drowned Río Azote Caballo, 66–70 m, *Dodge et al. 16869* (MO). Near Río Medio, *Miller 1745* (US). Pipeline road NNW of Gamboa near the Limbo Hunt Club, *Montgomery* (MO). Forest along the Río Indio de Gatún, sea level, *Pittier 2809* (US). Lake shore along Gatún River valley, *Pittier 6514* (US), *6744* (US). 12 mi S of Colón on Río Providencia, *Tyson & Blum 3946* (SCZ). Salamanca Hydrographic Station, Río Pequení, 80 m, *Woodson et al. 1576* (F, MO, NA, NY). CHIRIQUÍ: Burica Peninsula, San Bartolo Limite, 18 km W of Puerto Armuelles, 450 m, *Busey* 583 (F, MO). Half way between Progreso and Puerto Armuelles, *Croat 21879* (MO, NY). Haras San Miguel just N of Concepción, *Folsom 3945* (MO). Burica Peninsula, Quebrada Melliza, 6 mi S of Puerto Armuelles, 0–150 m, *Liesner 499* (MO). COLÓN: Orillas de una quebrada que desemboca en el Río Salud, cerca el puente de mismo nombre, *Carrasquilla & Taymes 144* (DUKE, MO, PMA). 3 mi de Portobelo, *Correa & Dressler 1758* (MO, PMA). Beach front strand vegetation near Portobelo, *Croat 14125* (MO, US). Nuevo Tonosí 2 mi from Portobelo on road to Nombre de Dios, 100 m, *Croat 33518* (MO). Río Indio on road from Portobelo to Nombre de Dios, 50 m, *Croat 33611* (MO). Río Guanche, *D'Arcy 9715* (MO). Hills just N of the Río Guanche, 1–200 m, *Davidse & D'Arcy 10076* (MO, US). Road from Colón to Portobelo, Río Guanche, *Folsom 3768* (MO). Beach along Portobelo road, *Gentry 726* (MO). Near Peluca, km 25.6 from Transisthmian Highway on the road to Nombre de Dios, upstream on tributary to Río Boqueron, *Kennedy 2670a* (DUKE, MO). Santa Rita Ridge road, right fork of road on property of Peter & Leslie Tassel, ca. 1.9 km from Boyd-Roosevelt Highway, *Mori & Kallunki 1797* (MO). Road to Mosquera from Palmas Bellas nearer Mosquera, *Mori & Kallunki 1957*

(MO). Forest around Portobelo, 5–100 m, *Pittier 2464* (US). Achiote, 30 m, *Skog & Butcher 4105* (US). PANAMÁ: Near archeological site at edge of Madden Lake, *Gentry & Tyson 5042* (MO). SAN BLAS: Río Ailigandí, *Duke 10848* (MO, OS). Ailigandí, *Dwyer 6860* (MO). VERAGUAS: Río Primero Braso, 2.5 km beyond Agriculture School Alto Piedra near Santa Fé, 700–750 m, *Croat 25465* (MO).

5. **Codonanthe uleana** Fritsch, Bot. Jahrb. Syst. 37: 492. 1906. TYPE: Río Jurua, Brazil, *Ule 5617* (B, no longer extant; HBG, designated lectotype by Wiehler, 1975b).

Columnea calcarata J. D. Smith, Bot. Gaz. (Crawfordsville) 33: 254. 1902. TYPE: Cubilquitz, Guatemala, *Tuerckheim 7645* (US, holotype; GH, isotype).

Codonanthe decurrens I. M. Johnst., Sargentia 8: 275. 1949. TYPE: Based on *Columnea calcarata* J. D. Sm., not *Codonanthe calcarata* (Miq.) Hanst.

Epiphytic vinelike *shrubs* or *subshrubs*; stems erect to ascending or pendulous, elongate, woody, thick, 3–6 mm or more in diam., green or reddish, densely puberulent, the nodes thickened and bearing adventitious roots. *Leaves* equal in a pair, lanceolate to more usually oblanceolate, or obovate, 2.5–7.0 cm long, 1.0–3.5 cm wide at the widest part, thick, membranous to subcoriaceous, the apex acute, the base cuneate, shallowly toothed, especially toward the apex, rarely entire, above dark dull green, glabrous or minutely glandular, below lighter green or suffused with red, glabrous with a few but prominent red or green extrafloral nectaries; petioles 3–10 mm long, glandular puberulent. *Inflorescences* axillary, of 1–3 flowers; peduncles lacking; pedicels curved, winged, 1–2 cm long, narrow below, but broader above, green, glabrous or minutely glandular puberulent. *Flowers* with the calyx somewhat bilabiate, the dorsal lobe curved around the corolla spur, the lobes winged or keeled dorsally and decurrent into the pedicel, narrowly triangular, 1.5–6 mm long, elongating in fruit, 1–2 mm wide at the base, green or reddish, glandular puberulent, reddish nectaries borne at the sinuses of the lobes; corolla white or white with red or yellow patches or reddish streaks, horizontal in the calyx tube, 2.5–3.8 cm long, the tube base with a large spur, narrowed above the spur then gradually broader above and subventricose below the throat, 4–10 mm broad, the outside glabrous to glandular, the limb subbilabiate, oblique, the lobes erect to spreading, 2–4 mm long and wide, obtuse, entire; stamens included, the filaments ca. 2 cm long, slender, sparsely glandular pubescent, the anthers coherent in 2 pairs, the anther sacs well separated on a wide connective, the pores ornamented with 2 hornlike projections; disc reduced to a bilobed, white gland impressed into the back of the ovary; ovary and style puberulent, the stigma stomatomorphic. *Capsule* fleshy, ovoid, 1 cm or more in diam., red or purple, atop the strongly curved pedicel; seeds oblong, striate, dark brown. *Chromosomes* $n = 16$ (Morley, 1967, as *C. decurrens*; Wiehler, 1975b).

Codonanthe uleana is distinctive by its keeled decurrent calyx lobes, its horned anthers and usually serrate leaves. The range of the species is quite large, from México through Central America to Colombia, as well as Amazonas, Brazil where the type was collected, and Peru and Bolivia. In Panamá, it has been collected in the provinces of Colón, Panamá, and San Blas, as well as the Canal Zone.

CANAL ZONE: Barro Colorado Island, *Croat 5619, 8269, 9429* (all MO); *Kenoyer 540* (US); *Wilson 65* (F, MO); Frijoles, *Stevens 1292* (US). COLÓN: East ridge, *Duke 15345* (OS). Santa Rita Ridge, highway to 8 mi E, 800 ft, *Dwyer et al. 9029* (MO). Santa Rita Ridge, ca. 5.5–6 mi E of Transisthmian Highway, *Lewis et al. 5380* (MO, SCZ). Lumber road 8 mi NE of Santa Rita along ridge, at 650 ft, *Wilbur & Weaver 10866* (DUKE). Without locality, *Duke 15245* (MO). PANAMÁ: 10 km N of El Llano on the road to Cartí, 400 m, *Busey 920* (MO). Panamerican Highway near Jenené, Río Cañita, *Duke 3869* (MO). SAN BLAS: Permé, *Cooper 233* (F, NY, US). El Llano-Cartí Road, 24.5–25 km from Panamerican Highway near continental divide, *Mori & Kallunki 5534* (MO).

7. COLUMNEA[9]*

Columnea L., Sp. Pl. 638. 1753. TYPE: *C. scandens* L.

Achimenes P. Br., Civ. Nat. Hist. Jamaica 270, *tab. 30.* 1756, non Pers., Syn. Pl. 2: 164. 1806. TYPE: *A. major, herbacea, subhirsuta oblique assurgens* P. Br. = *Columnea fawcettii* (Urban) Morton.

Dalbergaria Tussac, Fl. Antill. 1: 141, *pl. 19.* 1811–13. TYPE: *D. phoenicea* Tussac = *Columnea sanguinea* (Pers.) Hanst.

Vireya Raf., Specchio 1: 194. 1814. TYPE: *V. sanguinolenta* Raf. = *Columnea sanguinea* (Pers.) Hanst.

Eusynetra Raf., Fl. Tellur. 2: 57. 1837. TYPE: *E. bicolor* Raf. = *Columnea hirsuta* Sw.

Glycanthes Raf., Sylva Tellur. 83. 1838. TYPE: *G. scandens* (L.) Raf. = *Columnea scandens* L.

Aponoa Raf., Sylva Tellur. 84. 1838. TYPE: *A. repens* Raf. = *Columnea scandens* L.

Trichantha Hook., Icon. Pl. 3: *tab. 666.* 1844. TYPE: *T. minor* Hook. = *Columnea minor* (Hook.) Hanst.

Collandra Lemaire, Fl. Serres Jard. Eur. 3: *tab.* 223. 1847. TYPE: *C. pilosa* Lemaire = *Columnea aureonitens* Hook.

Ortholoma (Benth.) Hanst., Linnaea 26: 184, 209. 1854. LECTOTYPE: *O. acuminatum* (Benth.) Hanst. = *Columnea acuminata* Benth.

Pentadenia (Planch.) Hanst., Linnaea 26: 187, 211. 1854. TYPE: *P. aurantiaca* (Decne. ex Planch.) Hanst. = *Columnea aurantiaca* Decne. ex Planch.

Pterygoloma Hanst., Linnaea 26: 188, 211. 1854. TYPE: *P. repens* (Hook.) Hanst. = *Columnea repens* (Hook.) Hanst.

Stenanthus Oerst. ex Hanst., Linnaea 26: 184, 209. 1854. TYPE: *S. heterophyllus* Oerst. ex Hanst. = *Columnea grata* Mort.

Stygnanthe Hanst., Linnaea 26: 185, 209. 1854. TYPE: *S. moesta* (Poepp.) Hanst. = *Columnea moesta* Poepp.

× *Colbergaria* Wiehl., Selbyana 1: 408. 1976.

× *Coltrichantha* Wiehl., Selbyana 1: 408. 1976.

× *Coltadenia* Wiehl., Selbyana 1: 409. 1976.

× *Daltrichantha* Wiehl., Selbyana 1: 409. 1976.

× *Daltadenia* Wiehl., Selbyana 1: 409. 1976.

× *Trichadenia* Wiehl., Selbyana 1: 409. 1976, illegitimate name. Later homonym of *Trichadenia* Thwaites (Flacourtiaceae).

Perennial suffrutescent or succulent *herbs* or small *shrubs*, stems often having adventitious roots at the nodes, epiphytic or terrestrial, habit erect, spreading, prostrate or pendulous. *Leaves* opposite, more or less petiolate, those of a pair equal to strongly unequal; blades various in shape, usually with a characteristic indumentum. *Flowers* axillary, sometimes showy, more or less pedicellate,

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[9] This treatment was adapted extensively from a preliminary manuscript prepared in 1973 by Brian D. Morley, Assistant Director, Botanic Garden, North Terrace, Adelaide, South Australia 5000. This contribution by Dr. Morley, his subsequent comments and help are gratefully acknowledged. *Columnea oxyphylla* J. D. Smith has recently been discovered in Coclé Province.

* If *Tricantha citrina* Wiehl., Selbyana 5: 92. 1978, is determined upon examination of the type to be a distinct species, it will be transferred to *Columnea*. See *Columnea chiricana* Wiehl., Selbyana 5: 77. 1978.

bracteate but the bracts sometimes soon caducous; calyx lobes 5, free nearly to the base in most cases, mostly equal, the margins entire, toothed, or pectinate; petals 5, normally fused into a tubular or ventricose corolla tube with slightly to strongly unequal (zygomorphic) free corolla lobes, the 2 posterior lobes connate and themselves fused to 2 lateral lobes, the single anterior lobe being the least fused when flowers zygomorphic, the corolla lobes erect, spreading or reflexed, the tube gibbous at the base; stamens 4, the filaments brifely connate at the base and adnate to the base of the corolla tube, the anthers coherent in 2 pairs, exserted or included, the loculi dehiscent by longitudinal slits; disc normally reduced to a single bilobed gland or rarely 5 separate glands, the gland appressed to the posterior side of the ovary; ovary superior, unilocular, with 2 parietal placentas, the style terminal, about as long as the stamens, the stigma bilobed or stomatomorphic, exserted or included. *Fruit* a white or colored berry, sticky inside; seeds small and numerous (often more than 100), spindle shaped, pale brown with darker tips, the testa obliquely striate; embryo straight.

Columnea includes about 160 species occurring only in the New World tropics and extending from México through Central America, through a number of Caribbean islands into northern South America, and as far south as Peru and Bolivia. Fifty species are found in Panamá. Flowering material is essential for the identification of most species. The following account is based mainly on dried flowering material, supplemented when possible by greenhouse grown plants originally from Panamá.

The genus is named for Fabius Columna (1567–1640) whose book published in 1592 was the first in botany with copper-plate illustrations.

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a. Corolla lobes 5 mm long or less, erect, spreading, or incurved; stamens not exserted; berry usually ovoid in large-leaved taxa (sect. *Collandra*).[10]
  b. Blade length of leaf pairs strongly unequal.
    c. Calyx lobes entire to serrate.
      d. Bracts minute or to ca. 3 mm long.
        e. Corolla less than 1 cm long ..... 34. *C. parviflora*
        ee. Corolla more than 2 cm long ..... 39. *C. pulchra*
      dd. Bracts large, 0.9–3.2 cm long.
        f. Leaves red-spotted beneath.
          g. Stems hirsute with erect hairs ..... 11. *C. crassa*
          gg. Stems strigose-sericeous with adpressed hairs ..... 10a. *C. consanguinea* var. *adpressa*
        ff. Leaves not red-spotted beneath ..... 10b. *C. consanguinea* var. *darienensis*
    cc. Calyx lobes deeply toothed.
      h. Pedicels 3–5 cm long ..... 9. *C. cerropirrana*
      hh. Pedicels less than 2.5 cm long.
        i. Leaves pilose or densely hirsute above, margins more or less toothed.
          j. Leaves red-tipped beneath; corollas no more than 20 mm long ..... 35. *C. pectinata*
          jj. Leaves not red-colored beneath; corollas more than 20 mm long.
            k. Ovary ridged, sericeous on the ridges; calyx lobes green with reddish hairs, 1–2 toothed ..... 49. *C. vittata*
            kk. Ovary not obviously ridged, pilose at least apically; calyx lobes red or orange, 3–6 toothed.
              l. Leaves coriaceous, 15–20 cm long, green at margin ..... 2. *C. ampliata*
              ll. Leaves membranous, but thick from thick indumentum, 15.5–32.6 cm long, with reddish hairs toward margin ..... 40. *C. purpurata*
        ii. Leaves glabrous to sparsely hirsute above, margins more or less entire.
          m. Calyx lobes densely brown hirsute, hairs often obscuring sepal teeth; leaves more than 20 cm long ..... 16. *C. florida*
          mm. Calyx lobes reddish pilose, teeth clearly visible; leaves less than 20 cm long ..... 44. *C. segregata*
  bb. Blade length of leaf pairs subequal.
    n. Disc glands reduced to a single bilobed gland or 2 connate glands; leaves pilose or hirsute above, below either green or dark red, veins prominent.

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[10] Key adapted for the most part from the preliminary treatment by Morley; for a discussion, typifications, and synonymies of the sections of *Columnea* see Morley (1976).

o. Corolla less than 2.0 cm long; leaves reddish below ..... 7. *C. calotricha*
oo. Corolla more than 2.1 cm long; leaves green below ..... 13. *C. dissimilis*
nn. Disc glands 4 or 5; leaves strigillose above, below light green with green or pink prominent veins ..... 3. *C. angustata*
aa. Corolla lobes more than 5 mm long, erect or spreading; stamens exserted or not; berry globose.
p. Corolla lobes subregular to zygomorphic, 10 mm long or less, rarely more.
q. Corolla tube gradually tapering from throat to gibbous base, at most slightly swollen in middle; stamens held within entrance to throat or slightly exserted; corolla lobes ovate to orbicular, sometimes with sinus appendages, hardly zygomorphic; sepals various in shape (sect. *Pterygoloma*).
r. Leaves glabrous above ..... 28. *C. moorei*
rr. Leaves pilose or hirsute above.
s. Leaves green beneath, although sometimes red hirsute.
t. Calyx lobes ca. 23 mm long, red purple hirsute .... 46. *C. silvarum*
tt. Calyx lobes less than 10 mm long, brown hirsute .. 38. *C. polyantha*
ss. Leaves red purple spotted or concolorous beneath.
u. Disc glands 5 ..... 41. *C. rubida*
uu. Disc gland single and bilobed.
v. Corolla yellow and striped maroon ..... 21. *C. illepida*
vv. Corolla not striped.
w. Corolla glabrous or at most puberulent; calyx lobes 10 mm or more long ..... 37. *C. perpulchra*
ww. Corolla pilose with long hairs; calyx lobes 9 mm long or less ..... 12. *C. cruenta*
qq. Corolla tube ventricose (notably constricted near throat and base); stamens not normally exserted; corolla lobes various to almost linear, more or less zygomorphic; sepals often acuminate (sect. *Ortholoma*).
x. Leaves pilose or hirsute above.
y. Leaves green beneath; corollas red throughout ..... 4. *C. anisophylla*
yy. Leaves red purple beneath; corollas red or red and yellow.
z. Pedicels 5 cm long or more; corollas red with posterior lobes yellow ..... 36. *C. pendula*
zz. Pedicels less than 3 cm long, corollas red or red and yellow.
A. Stem yellow brown villous, corollas red ..... 31. *C. ochroleuca*
AA. Stem red purple hirsute; corollas yellow with red brown stripes ..... 27. *C. mira*
xx. Leaves glabrous above.
B. Stems strigose with adpressed hairs ..... 43. *C. sanguinolenta*
BB. Stems villous to hirsute with erect hairs ..... 45. *C. serrata*
pp. Corolla lobes strongly zygomorphic, more than 10 mm long.
C. Corolla tube straight and gradually tapering from throat to base; disc glands 2, dorsally connate, or 1 and bilobed; stamens exserted (sect. *Columnea*).
D. Calyx lobes more than 30 mm long, serrate-laciniate; leaf blades 21–28 cm long, 2–3 cm wide, apex long-attenuate ..... 17. *C. gallicauda*
DD. Calyx lobes less than 30 mm long, if longer then not serrate-laciniate; leaf blades usually much shorter than 20 cm long, apex not long attenuate.
E. Corollas white sericeous; calyx lobes with a sericeous midrib and often with broad ovate base and attenuate tip remotely toothed; pedicels sericeous.
F. Corolla deep red with rich yellow throat; leaves all green or flushed with red; calyx lobes green or reddish ..... 30. *C. nicaraguensis*
FF. Corolla completely yellow; leaves dark red at apices; calyx lobes yellow ..... 8. *C. canarina*
EE. Corollas and calyx lobes not as above; corollas either glabrous, pilose or strigose, not white, sericeous; sepals either glabrous, pilose, or hirsute at the midrib, variously shaped; pedicels gla-

brous, pilose, hispid, or strigose (sepals and pedicels sometimes white sericeous in 14. *C. dressleri* and 48. *C. tulae*, but then corollas reddish pilose).

G. Leaves glabrous above.

H. Corollas yellow or predominantly yellow with red or pink stripes.

I. Calyx lobes ca. 3 cm long and half the length of the red-striped corolla ..... 23. *C. kalbreyeriana*

II. Calyx lobes less than 2 cm long (rarely to 2.5) and less than half the length of the corolla (rarely to half the length in *C. rubra*).

J. Lower leaf surfaces generally pink to maroon; calyx lobes red; corolla yellow throughout or less often with red stripes ..... 42. *C. rubra*

JJ. Lower leaf surfaces strongly reddish only toward apex or margin; calyx lobes greenish yellow or sometimes with a reddish mid-vein; corolla with prominent dark red stripes ..... 50. *C. zebrina*

HH. Corollas red or predominantly red with yellow throat.

K. Blade length of leaf pairs strongly unequal.

K′. Leaf tips green below ..... 14. *C. dressleri*

K″. Leaf tips red below ..... 50. *C. zebrina*

KK. Blade length of leaf pairs nearly equal.

L. Stems conspicuously hispid, especially at tip ..... 5. *C. arguta*

LL. Stems strigose.

M. Corolla throat 5–7 mm wide (tube slender); ovary glabrous in lower half ..... 6. *C. billbergiana*

MM. Corolla throat more than 7 mm wide; ovary sericeous to pilose in lower half.

N. Anterior corolla lobe more than 20 mm long; calyx lobes entire to subentire ..... 1. *C. allenii*

NN. Anterior corolla lobe less than 20 mm long; calyx lobes toothed (sometimes remotely) with teeth to 1 mm long.

O. Leaves 10–16 mm long, ovate to elliptic-ovate, the tip obtuse to acute ..... 32. *C. oerstediana*

OO. Leaves 15–33 mm long, ovate lanceolate, the tip acuminate ..... 47. *C. tenuis*

GG. Leaves hirsute, pilose, or tomentose above.

P. Calyx lobes toothed, teeth 1.5–3.0 mm long.

Q. Leaves tomentose above ..... 48. *C. tulae* var. *tomentulosa*

QQ. Leaves strigose or pilose hirsute above.

R. Corolla red; leaves less than 5 cm long ..... 15. *C. flaccida*

RR. Corolla red and yellow; leaves usually more than 5 cm long.

S. Corolla yellow with red spots and stripes; leaves much more than 5 cm long; galea bilobed ..... 24. *C. maculata*

SS. Corolla red with yellow throat; leaves variable in length; galea truncate ..... 25. *C. magnifica*

PP. Calyx lobes entire or remotely serrulate, teeth to 1 mm long.

T. Leaves 5.5–10.1 cm long; corollas red with yellow stripes; stems long hirsute ..... 19. *C. hirsutissima*

TT. Leaves 1.2–3.2 cm long; corollas not striped when red and yellow; stems strigose or short hirsute.

U. Pedicels to 5 mm long.

V. Stems red hirsute; staminal filaments pilose ..... 20a. *C. hirta* var. *hirta*

VV. Stems orange hirsute; staminal filaments nearly glabrous .. 20b. *C. hirta* var. *mortonii*

UU. Pedicels more than 5 mm long.

W. Petioles 3–10 mm long; anterior lobe of corolla less than 20 mm long ..... 33. *C. panamensis*

WW. Petioles 1–2 mm long; anterior lobe of corolla more than 25 mm long ..... 26. *C. microcalyx*

CC. Corolla tube curved and more or less ventricose; disc glands 4 or 5 and free, or 2 and dorsally connate, or 1 and bilobed; stamens exserted (sect. *Pentadenia*).

X. Leaves glabrous to sparsely strigose above; calyx lobes more than 20 mm long ..... 22. *C. incarnata*

XX. Leaves pilose or tomentose above; calyx lobes less than 20 mm long.

Y. Corolla 4 cm long or less; disc glands 5 ..... 29. *C. nervosa*

YY. Corolla 6.0–7.5 cm long; disc gland single and bilobed.

Z. Leaves oblanceolate; calyx lobes subentire to serrate ..... 25. *C. magnifica*

ZZ. Leaves narrowly elliptic; calyx lobes serrate laciniate ..... 18. *C. hiantiflora*

1. **Columnea allenii** Morton, Ann. Missouri Bot. Gard. 29: 42. 1942. TYPE: Panamá, *Allen 2179* (US, holotype; US, isotype).

Epiphytic *herbs*; stems woody at the base, pendent, 1–2 mm in diam., reddish, strigose. *Leaves* of a pair equal, oblong elliptic, 1.5–2.2 cm long and 8–10 mm wide, the apex short acuminate, rounded at the base, entire, green above, glabrous, beneath green or sometimes reddish, sparsely strigose, hairs reddish, 4–9 celled, more numerous on the veins, redder near the margins, also with 2–3 celled transparent hairs; petioles 1–2 mm long. *Flowers* solitary; bracts to 1 mm long, linear, strigose; pedicels 10–17 mm long, reddish strigose; calyx lobes ovate lanceolate, 2.0–2.9 cm long, long acuminate, subentire, green tinged with red, adpressed pilose; corollas scarlet with yellow streaks at sinuses of the anterior lobes and sometimes on the lateral lobes, funnelform but strongly zygomorphic, 6.2–7.1 cm long, ca. 4 mm in diam. above the base, becoming 15 mm at the throat, the lobes strongly unequal, the posterior pair connate, truncate at the apex, 2.0–2.5 cm long, the lobed portion of the corolla 3.7–4.5 cm long, the anterior lobe 2.3–2.6 cm long, reflexed, the corolla externally densely reddish pilose; stamens exserted, the filaments yellow, glabrous; ovary pilose, the style slightly glandular pilose, yellow, the stigma bilobed. *Fruits* not seen. *Chromosomes* $2n = 18$ (Fussell, 1958).

This species is known only from Panamá from north of El Valle, Province of Coclé.

COCLÉ: Hills N of El Valle de Antón, 1000 m, *Allen 2179* (US). El Valle de Antón, North Hills, *Allen 3554* (BM, MO, US). WITHOUT LOCALITY: *Allen 2485* (GH).

2. **Columnea ampliata** (Wiehl.) L. Skog, comb. nov.

Dalbergaria ampliata Wiehl., Selbyana 2: 101, *pl. 30A*. 1977. TYPE: Buenos Aires, N slope of ridge E of Cerro Tute, NW of Santa Fé, Province of Veraguas, Panamá, *Dressler 5543* (SEL, holotype, not available for study).

Epiphytic *herbs* or *subshrubs*; stems erect, ascending, or spreading, to 40 cm long, to 1 cm in diam., the internodes villous hirsute; branches few. *Leaves* unequal in a pair; larger leaves oblanceolate, 15–20 cm long, 6–8 cm wide, coriaceous, the apex acuminate, the base oblique, the margin denticulate, above and below pilose; petiole 0.5–1.5 cm long, hirsute; smaller leaves similar but smaller, ca. 3 cm long, and 1 cm wide. *Inflorescences* axillary, cymose, few flowered; peduncles lacking; bracts lanceolate, ca. 1 cm long, 0.4 cm wide; pedicels 0.7–1.0 cm long, densely villous. *Flowers* with the calyx lobes narrowly lanceolate and laciniate or pectinate, ca. 3.2 cm long, and 2 cm wide, the teeth 5–6 on each side, narrow, each ca. 1 cm long, red, pilose to sericeous; corolla red or yellow striped, erect in the calyx, the tube gibbous at the base, 3.4–4.2 cm long, ca. 1 cm wide, the outside pilose above, the lobes of the limb triangular, ca. 2 mm long and wide, red, inside glabrous; stamens not exserted, the filaments 2.5–3.5 cm long, adnate for ca. 1 mm to corolla tube, glabrous, the anthers oblong; disc reduced to a bilobed posterior gland; ovary apex pilose, the style 2–3 cm long, glabrous, the stigma stomatomorphic. *Fruits* not seen.

The above description is adapted from the original; no specimens were seen of this species.

3. **Columnea angustata** (Wiehl.) L. Skog, comb. nov.

Pentadenia angustata Wiehl., Selbyana 2: 118. 1977. TYPE: Old road from Cali to Buenaventura, 8 km past La Elsa, Dept. El Valle, Colombia, *Wiehler et al. 7276* (SEL, holotype, not available for study).

Epiphytic *subshrubs* or *shrubs*; stems erect, ascending, or pendent, ca. 0.5 m long and 1 cm in diam. below, rooting from the prominent nodes, the internodes reddish, sericeous above, scaly below. *Leaves* nearly equal in a pair, elliptic, 4.5–8.5 cm long, 1.2–3.0 cm wide, membranous, the apex acute, the base cuneate, not oblique, entire, above dark green, strigillose, below lighter green with green or pinkish prominent veins, sericeous; petioles 1–2 cm long, green or reddish, sericeous. *Inflorescences* axillary, often at the nodes of fallen leaves somewhat below the apex, cymose but few flowered; peduncles lacking; bracts reddish, sericeous; pedicels 2–3 mm long. *Flowers* with the calyx lobes erect, narrowly lanceolate, 0.6–1.2 cm long, acuminate, toothed, almost laciniate, pink, sericeous; corolla yellow or yellow orange, erect in the calyx, the tube gibbous at the base, curved, slender, ca. 2 cm long and 4 mm wide at the middle, sericeous with red-

dish hairs, the lobes triangular; stamens included or rarely exserted, the filaments glabrous, the anthers orbiculate; disc reduced to 4 or 5 glands; ovary ovoid, pubescent, the style sparsely pubescent, the stigma bilobed. *Berry* white, pilose, surrounded by the persistent calyx; seeds oblong, striate, dark brown, shiny.

Columnea angustata apparently ranges from Costa Rica to Colombia. In Panamá, the species is known from middle elevations from the provinces of Darién and Veraguas. It may be expected in other areas as well.

DARIÉN: Cloud forest, Cerro Campamiento S of Cerro Pirre, *Duke 15614* (US). N slopes of Cerro Pirre, lower montane cloud forest, 700–950 m, *Mori & Kallunki 5471* (MO). VERAGUAS: Primary forest, 0.6 mi beyond Escuela Agricola Alto Piedra, 730 m, *Croat & Folsom 34005* (MO). 5 mi W of Santa Fé on road past Escuela Agricola Alto Piedra on Pacific side of divide, 800–1200 m, *Liesner 916* (MO).

4. **Columnea anisophylla** DC., Prodr. 7: 542. 1839. TYPE: "America australi," *Poeppig 1080* (G-DC; IDC 800. 1362: III. 5).

Nematanthus heterophyllus Poepp. in Poepp. & Endl., Nov. Gen. Sp. Pl. 3: 4, *tab. 203*. 1840. TYPE: Pampayaco, Peru, *Poeppig 1080* (W, holotype, photo, US).
Ortholoma vestitum Klotzsch ex Oerst., Cent. Gesn. 51. 1858. TYPE: "Costa Rica and Veragua," *Warscewicz 21* (193) (not seen).
O. warscewiczianum Klotzsch ex Oerst., Cent. Gesn. 51. 1858. TYPE: "Costa Rica and Veragua," *Warscewicz 30* (K, L, P, isotypes).
Columnea warscewicziana (Klotzsch ex Oerst.) Hanst., Linnaea 34: 392. 1865.
Ortholoma anisophyllum (DC.) Wiehl., Phytologia 27: 320. 1973.
Trichantha anisophylla (DC.) Wiehl., Selbyana 1: 34. 1975.

Epiphytic *herbs*; stems 3–5 mm in diam., pale or dark brown, villous or hirsute. *Leaves* of a pair strongly unequal, the larger leaves lanceolate to oblanceolate, 7.3–14.7 cm long and 1.8–3.4 cm wide, the apex acuminate, strongly oblique at the base, more or less serrate, green above, densely hirsute, hairs brown, 4–6 celled, more numerous on the midrib and the veins, beneath green, densely hirsute, hairs brown, 5–8 celled, more numerous on the midrib and the veins, also 2–3 celled white adpressed hairs; petioles 1–3 mm long; smaller leaves lanceolate, 0.9–1.8 cm long and 2–7 mm wide, acuminate, oblique at the base, green. *Flowers* solitary or paired; bracts 2.5–4 mm long, linear, entire, brown hirsute; pedicels 2.3–3.8 cm long, brown hirsute; calyx lobes lanceolate, 0.8–1.3 cm long, long acuminate, irregularly subulate toothed, the lobes to 1 mm long, green brown hirsute; corollas scarlet outside, the inside yellow, ventricose, 3.3–5.4 cm long, ca. 5 mm in diam. above the base, becoming ca. 1.9 cm in diam., contracted at the throat to ca. 1.0 cm in diam., the lobes unequal, the posterior pair partly connate, remainder spreading and 0.7–1.0 cm long, the corolla externally sparsely reddish pilose, internally glabrous; filaments yellow, pilose, the anthers included; ovary sericeous, the style yellow, glabrous, the stigma stomatomorphic. *Fruits* ovoid, ca. 1.0 cm in diam.; seeds fusiform, 1 mm or more long, twisted, yellow to brown. *Chromosomes* $2n = 18$ (Sherk, 1960).

Columnea anisophylla is known from Costa Rica to Peru, in Panamá from the province of Chiriquí, where it grows in rain forest.

CHIRIQUÍ: Bajo Mono-Róbalo Trail, W slopes of Cerro Horqueta, 5000–7000 ft, *Allen*

4833 (GH, MO, NY, US). Cerro Horqueta, 7000 ft, *Blum & Dwyer* 2595 (F, FSU, MO, MO, SCZ). Bajo Chorro, Río Caldera, *Butcher s.n.* (US). Bajo Chorro, 6000 ft, *Davidson 406* (GH, MO, US). Road from Boquete to Finca Lérida, 2000 m, *Dressler & Williams 4011* (MO, PMA). Upper Caldera River above El Boquete, 1450–1650 m, *Maxon 5703* (US). Cuesta de Las Palmas, S slope of Cerro de la Horqueta, 1700–2100 m, *Pittier 3215* (US, US). 5 km NE of Boquete, 1700–1800 m, *Skog et al. 4035, 4040* (both MO, US). Above Río Caldera beyond Bajo Mono, 1800 m, *Wilbur et al. 11064* (DUKE, MO). Above village of San Ramón near Bajo Mono, 4 mi NW of Boquete, 6000 ft, *Wilbur et al. 13539* (DUKE). Bajo Mono and Quebrada Chiquero, 1500 m, *Woodson & Schery* 598 (MO).

5. **Columnea arguta** Morton, Ann. Missouri Bot. Gard. 29: 43. 1942. TYPE: Panamá, *Allen 2336* (US).

C. consimilis Morton, Proc. Biol. Soc. Wash. 69: 194. 1956. TYPE: Panamá, *Allen 4380* (MO, holotype; US, isotype).

Woody based *herbs*, epiphytic; stems pendent, 1.5–3.0 mm in diam., red glandular hispid when young. *Leaves* of a pair equal, ovate lanceolate or lanceolate, 1.6–3.1 cm long and 6–12 mm wide, acute to long acuminate, cuneate to rounded at the base, entire, above green or reddish, glabrous, beneath pale green or reddish, sparsely strigose especially on the margins, the hairs transparent or reddish, 4–5 celled, few glandular hairs, also 2–3 celled appressed hairs; petioles 1–3 mm long. *Flowers* solitary or paired; bracts to 1.5 mm long, red strigose; pedicels 5–15 mm long, red hispid; calyx lobes erect, lanceolate, 1.1–2.3 cm long, 3–7 toothed, the teeth to 7 mm long, yellowish green or green tinged with red, reddish hirsute; corollas scarlet or orange red with yellow running from the sinuses of the lobes, funnel shaped but strongly zygomorphic, 4.6–7.2 cm long, ca. 4 mm in diam. above the base, becoming ca. 10 mm in diam. at the throat, the lobes strongly unequal, the posterior pair connate, emarginate at the apex, 1.2–3.3 cm long, ca. 3.5 mm in diam. above the base, becoming 10 mm in diam. at the throat, the lobed portion of the corolla ca. 3.6 cm long, the anterior lobe 1.0–2.1 cm long, reflexed, the corolla externally reddish pilose, internally glandular at the base; filaments glabrous above, yellow, the anthers exserted; ovary sericeous, the style glandular, yellow, the stigma bilobed. *Fruits* not seen. *Chromosomes* $2n = 18$ (Fussell, 1958).

This species is known only from Panamá from the provinces of Coclé, Colón, Darién, Panamá, and Veraguas, at 10–1,000 m in damp forest.

COCLÉ: Hills N of El Valle de Antón, La Mesa, 1000 m, *Allen 2336* (US). Region N of El Valle de Antón, La Mesa, 1000 m, *Allen 2795* (US), *3718* (MO, US). Foothills of Cerro Pilón near El Valle, 900 m, *Duke & Correa 14677* (MO, REED). 3 km NE of El Valle, *Mori & Kallunki 2951* (MO). La Mesa ca. 5 mi N of El Valle, *Wilbur & Luteyn 17736* (DUKE). COLÓN: Santa Rita lumber road ca. 15 km E of Colón, *Dressler 3746* (DUKE, PMA); *Dressler & Lewis 3730* (MO, PMA). Santa Rita Ridge road 4 mi from Transisthmian Highway to Agua Clara weather station, 500 m, *Gentry et al. 8866* (MO). 2–3 mi up the Río Guanche, 10–20 m, *Kennedy & Foster 2133* (MO). Santa Rita Ridge, end of road from Transisthmian Highway, ca. 10 mi from highway, *Porter et al. 4768* (MO). Old logging road above Río Iguanita, 390 m, *Skog et al. 4190* (E, MO, US). DARIÉN: Headwater of Río Tuquesa ca. 2 km air distance from Continental Divide, upper gold mining camp of Tyler Kittredge, *Croat 27153* (MO). PANAMÁ: Newly cut road from El Llano to Cartí-Tupile, 12 mi above Panamerican Highway, 200–500 m, *Croat 22868* (MO). Region of Cerro Jefe, *Dressler 3065* (MO, PMA). El Llano to Cartí Road, *Folsom & Collins 1506* (MO, US). 18.2 km E of Cerro Azul village (Goofy Lake), 800–900 m, *Gentry & Mori 13423* (MO). 10–20 km above Panamerican Highway on road from El Llano to Cartí-Tupile, 400–500 m, *Kennedy 2717* (MO); *Luteyn & Wilbur 4675*

(DUKE); *Mori & Kallunki 2244* (MO, PMA); *Mori & Kallunki 2866* (MO). Gorgas Memorial Labs yellow fever research camp ca. 25 km NE of Cerro Azul on Río Piedras, 550 m, *Mori & Kallunki 3274* (MO). El Llano-Cartí road, 8–12 km from Panamerican Highway, 1100–1200 ft, *Mori et al. 4156* (MO); *Nee & Warmbrodt 10395* (MO); *Wilbur & Luteyn 19497* (DUKE). VERAGUAS: Slopes of Cerro Tute, Santa Fé, 2500 ft, *Allen 4830* (MO, US). 6.4 km outside of Santa Fé on the road toward the cordillera, *Folsom 2987* (MO).

6. **Columnea billbergiana** Beurl., Kongl. Vetensk. Acad. Handl. 1854: 135. 1854. TYPE: Panamá, *Billberg* (S, holotype).—FIG. 8.

C. percrassa Morton, Baileya 7: 59. 1959. TYPE: Panamá, *Allen 2432* (US).

Woody based *herbs* or *subshrubs*, epiphytic; stems 2–5 mm in diam., green to reddish, more or less transparent strigose when young. *Leaves* of a pair subequal, ovate elliptic to lanceolate, 1.8–3.7 cm long and 8–18 cm wide, fleshy, acute or rounded at the apex, cuneate at the base, entire, green above, glabrous, beneath pale green to red, strigose, hairs transparent, 4–7 celled, more numerous on the veins, both adpressed and erect, also 2–3 celled white appressed hairs; petioles 2–6 mm long. *Flowers* solitary; bracts, 3–6 mm long, linear, strigose; pedicels 5–13 mm long, green or reddish transparent or reddish adpressed pilose; calyx lobes ovate lanceolate, 8–19 mm long, acuminate, entire to remotely denticulate, green or reddish, sparsely strigose but more dense on the midrib; corollas scarlet or orange red, often with yellow running from sinuses of the anterior lobe to the base of the corolla, funnelform but strongly zygomorphic, 4.5–7.0 cm long, ca. 3 mm in diam. above base, becoming ca. 6(–10) mm in diam. at the throat, the lobes strongly unequal, posterior pair connate, apiculate, 7–16 mm long, the lobed portion of the corolla 2.2–3.3 cm long, the anterior lobe 1.2–1.9 cm long, reflexed, externally sparsely reddish pilose; filaments red, glabrous or rarely glandular, the anthers exserted; ovary pilose, the style exserted, ca. 6 cm long, yellow or reddish, glandular pilose, the stigma bilobed. *Fruits* ovoid, ca. 1.4 cm in diam., white; seeds fusiform, yellow brown. *Chromosomes* $2n = 18$ (Lee, 1962).

This species is known only from Panamá but is common from the Canal Zone and the provinces of Coclé, Colón, Darién, Panamá, and Veraguas.

CANAL ZONE: Barro Colorado Island, *Brown 93* (F); *Croat 10088* (DUKE, MO), *10935* (MO); *Ebinger 193* (MO, US); *Foster 1069* (DUKE); *Shattuck 556* (F, MO). Lion Hill Station, *Hayes* (BM). Garden of C. W. Powell, Balboa, said to come originally from Frijoles, *Maxon 6553* (US). Gatún River valley, *Pittier 6516* (US). COCLÉ: El Valle de Antón, 600–1000 m, *Allen 1651* (GH, MO, US), *2149* (MO, US), *2309* (US), *2353* (MO, US), *3412* (BM, MO, US). Flat forested area below Cerro Pilón, *Croat 13459* (MO). Cloud forest on slopes of Cerro Pilón near El Valle, 700–900 m, *Duke 12050, 12084* (both MO, REED) *12165* (MO). La Mesa at El Valle de Antón, *Folsom & Butcher 2823* (MO); *Gentry 7415* (MO). El Valle de Antón, Río Indio trail, 500–700 m, *Hunter & Allen 303* (BM, MO, US). Mountains beyond La Pintada, 400–600 m, *Hunter & Allen 564* (MO, US). El Valle de Antón, La Mesa, 1000 m, *Kennedy et al. 3008* (MO). Mountains N of El Valle de Antón, 2500–3000 ft, *Lewis et al. 1766* (MO). Foot of Cerro Pilón above El Valle de Antón, 2000 ft, *Porter et al. 4356* (MO, SCZ), *4613* (MO). COLÓN: Santa Rita Ridge, 15 mi E of Colón, 1200 ft, *Butcher* (US). 1 mi from Portobelo, *Correa & Dressler 1763* (DUKE, F, MO, PMA). Santa Rita lumber road, ca. 15 km E of Colón, *Dressler 4036* (MO, PMA); *Dressler & Williams 3970* (PMA). Santa Rita Ridge near Agua Clara rainfall station, *Foster 1732* (DUKE, MO, PMA). Santa Rita Ridge ca. 5.5–6.0 mi E of Transisthmian Highway, *Lewis et al. 5374* (MO). 10 mi SW of Portobelo, 2–4 mi from coast, 10–200 m, *Liesner 1085* (FSU, MO). River 3 mi E of Portobelo, 20 m, *Liesner 1114* (DUKE, MO, USF). Río Guanche, ca. 2.5 km upriver from

bridge on road to Portobelo, *Mori et al. 6459* (MO, US). Río Guanche ca. 3 km upriver from bridge on road to Portobelo, 25 m, *Mori & Kallunki 5219* (MO). Achiote, 30 m, *Skog & Butcher 4103* (US). DARIÉN: Cerro Pirre, *Bristan 472* (MO). Headwater of Río Tuquesa ca. 2 km air distance from Continental Divide, upper gold mining camp of Tyler Kittredge, *Croat 27104, 27274* (both MO). Between Upper Río Membrillo and Camp 7 on construction road to San Blas, 100–800 m, *Duke 10894* (MO). Cerro Mali base camp near Colombian border, 1500 m, *Gentry & Mori 13786* (MO, PMA). N slopes of Cerro Pirre, 700–950 m, *Mori & Kallunki 5459* (MO, US). PANAMÁ: Cerro Campana, 1000 m, *Allen 2428* (MO, US), *2432* (US). Cerro Jefe beyond La Eneida, *Correa & Dressler 807* (MO, PMA). Road to Cerro Campana, *Croat 14684* (MO, NY). Campo Tres, 3 mi NE of Altos de Pacora, 500–800 m, *Croat 22700* (MO). El Llano-Cartí road, 5–12 km from Panamerican Highway, 350–400 m, *Croat 25159, 25171, 34765* (all MO). Middle slopes of Cerro Campana ca. 1 mi from Panamerican Highway, 150 m, *Croat 35959* (MO). Cerro Campana, *Dressler 4021* (PMA). El Llano-Cartí highway, 10 km N of El Llano, *Dressler 4371A* (PMA). Cerro Jefe, headwaters of Río Cascadas, 700 m, *Dressler & Williams 4016* (MO, PMA). Cerro Jefe, 10–13 mi beyond Goofy Lake, *Duke 8013* (MO). Cerro Jefe, near Río Indio, 2100–2200 ft, *Duke 15210* (MO). La Eneida, region of Cerro Jefe, *Dressler 3469* (PMA). Cerro Jefe, 700 m, *Dressler 3848* (PMA); *Dwyer 7251* (MO); Cerro Jefe, *Dwyer et al. 5036* (MO); *Gentry 4881* (MO). Cerro Campana, 800–1000 m, *Gentry 4935* (MO, PMA). 4–6 mi N from Panamerican Highway just W of El Llano, *Gentry 5108* (MO). Cerro Campana, *Hutchinson & Dressler 2952* (MO, NY, US). 12–16 km above Panamerican Highway on road from El Llano to Cartí-Tupile, 150–400 m, *Kennedy et al. 3145* (MO). Cerro Campana, 2600–2800 ft, *Lewis et al. 1918* (MO), *1924* (MO); *Liesner 611, 625* (both MO). El Llano-Cartí-Tupile road 12 mi above Panamerican Highway, 200–500 m, *Liesner 1147* (MO, US), *1287* (MO). Cerro Campana, *Luteyn 1027* (DUKE). El Llano-Cartí road, 8–11 km from Panamerican Highway, 300–450 m, *Mori 7749* (MO); *Mori & Kallunki 5149* (MO, US); *Nee & Tyson 10952* (MO, MO). Cerro Campana *Porter et al. 4153* (MO, SCZ), *4222* (MO), *4273, 4948, 4959* (all MO); *Skog et al. 4152* (MO, US). El Llano-Cartí road 8–16 km from El Llano and the junction with the Panamerican Highway, 500 m, *Skog & Folsom 4160* (MO, US), *4165* (E, MO, US), *4166* (US), *4167* (MO, US), *4170* (US). VERAGUAS: Río Primero Brazo 2.5 km beyond Escuela Agricola Alto Piedra near Santa Fé, 700–750 m, *Croat 25508, 25516* (both MO). Beyond Tres Brazos River along steep descent 11 km beyond Santa Fé, 650 m, *Croat 25614, 25637* (both MO). Caribbean slope above Río Primero Brazo 5 mi NW of Santa Fé, 700–1200 m, *Liesner 971* (MO). 10 km NW of Santa Fé on road to Calovébora at first branch of Río Santa María, *Mori & Bolton 7622* (MO). WITHOUT LOCALITY: *Billberg* (S).

7. **Columnea calotricha** J. D. Smith, Bot. Gaz. (Crawfordsville) 40: 9. 1905. TYPE: Cubilquitz, Dept. Alta Verapaz, Guatemala, *Tuerckheim 8542* (US, holotype; US, isotype).

Alloplectus calotrichus (J. D. Smith) Stearn, Bull. Brit. Mus. Nat. Hist. (Bot.) 4(5): 189. 1969.
Ortholoma calotrichum (J. D. Smith) Wiehl., Phytologia 27: 321. 1973.
Trichantha calotricha (J. D. Smith) Wiehl., Selbyana 1: 34. 1975.

Epiphytic or rarely terrestrial *herbs* or *shrubs*; stems erect or ascending, 0.1–1 m tall, reddish, hirsute, branches few. *Leaves* usually subequal, rarely strongly unequal, elliptic or obovate, 4–15 cm long, 1.5–6.0 cm wide, membranous, the apex acute to acuminate, the base cuneate, oblique, serrulate or crenulate, above dark green, pilose, below dark red, pilose; petioles to 3 cm long, green, pilose. *Inflorescences* axillary, 1–7 flowers in a fascicle; peduncles lacking; bracts lanceolate, 5–8 mm long; pedicels 3–10 mm long, reddish hirsute. *Flowers* with the calyx lobes distinct, nearly equal, oblanceolate or oblong, 1.0–1.8 cm long,

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FIGURE 8. *Columnea billbergiana* Beurl. Habit (×⅘). [After *Skog & Folsom 4167* (US).]

ca. 5 mm wide, acute and serrulate at the apex, red or orange, densely pilose; corolla orange yellow or yellow with reddish hairs, erect in the calyx, the tube 1.5–2.0 cm long, gibbous at the base, nearly straight, not ventricose, the outside pilose, the inside glabrous, the limb more or less erect, triangular, 3–4 mm long; stamens included, the filaments equalling the corolla tube, glabrous, the anthers suborbicular, coherent in pairs; disc of one large entire or bilobed gland; ovary ovoid, pubescent, the style glabrous, the stigma bilobed. *Fruit* ovoid to globose, ca. 1 cm across, white, sparsely pilose; seeds oblong, ca. 0.5 mm long, striate, light brown, shiny, the white funicle attached at base.

So far only known in Panamá from the provinces of Darién and Veraguas at about 700 m, *Columnea calotricha* is also reported from Guatemala, Costa Rica, Surinam and French Guiana. This species was recently brought into cultivation.

Columnea calotricha most closely resembles *C. pulchra*, but the latter species differs in having longer pedicels, longer lemon-yellow corollas, ca. 4 cm long, and usually green on the undersides of the leaves.

DARIÉN: Cerro Campamiento S of Cerro Pirre, *Duke 15678* (US), *15696* (US). Cerro Pirre, 2500–4500 ft, *Duke & Elias 13774* (MO). VERAGUAS: 0.2 mi beyond fork in road at Escuela Agricola Alto Piedra on road to Río Calovébora, 750 m, *Croat & Folsom 33871* (MO). Road between Santa Fé and Río Calovébora, 1.8 mi beyond Escuela Agricola Alto Piedra, 735 m, *Croat & Folsom 34277* (MO). Between second and third branches of Río Santa María, 10–12 km NW of Santa Fé, 650–750 m, *Dressler 5070* (PMA). 6.4 km outside of Santa Fé, *Folsom 2990* (MO). N of Santa Fé on property of Escuela Agricola Alto de Piedra, *Mori & Kallunki 2547* (MO). Road to agriculture school 3–4 km by road W of Santa Fé, 2500 ft, *Nee 11309* (MO).

8. **Columnea canarina** Wiehl., Selbyana 2: 98. 1977. TYPE: Cultivated, Marie Selby Botanical Gardens from plants collected in Prov. Chiriquí, Panamá, *Wiehler 77112* (SEL, holotype, not available for study).

Epiphytic *herbs* or *subshrubs*; stems erect, ascending or spreading, to 50 cm long, 0.5–1.2 cm in diam., the internodes green, becoming tawny with age, sericeous. *Leaves* strongly unequal in a pair, the larger leaf in a pair elliptic or oblanceolate, 12–20 cm long, 4.0–5.5 cm wide, the apex acuminate, the base oblique or obtuse, above dark green, shiny, sparsely strigose, below lighter green with red spots and apices, sparsely sericeous, more dense on the veins; petiole subsessile to 5 mm long, sericeous; the smaller leaves ca. 7 cm long and 3 cm wide. *Inflorescences* cymose, few flowered in the axils of the larger leaves; peduncles lacking; bracts lanceolate, ca. 2 cm long and 0.6 cm wide, entire, yellow, sericeous; pedicels 1.5–2.0 cm long, yellow, densely sericeous. *Flowers* with the calyx lobes nearly equal, lanceolate to elliptic, 2.8–3.6 cm long, 0.7–0.9 cm wide, the apex acuminate, the margin serrate, yellow, sericeous; corolla canary yellow, erect in the calyx, the tube spurred, ca. 6.5 cm long, the mouth of the tube oblique, galea 1.4 cm long and wide, the lateral lobes triangular, 1 cm long, the lower lobe somewhat reflexed, linear, 1.9 cm long, 0.5 cm wide, the outside of the tube pilose or sericeous, the inside glandular; stamens with the filaments adnate to the base of the corolla for ca. 2 mm, 5.7 cm long, glandular pubescent, the

anthers oblong, ca. 2 mm long; disc reduced to a bilobed posterior gland; ovary sericeous, style 6.2 cm long, glandular, the stigma bilobed to stomatomorphic. *Fruit* not seen.

As only a fragmentary specimen has been seen, the description is adapted from the original publication. Plants of *Columnea canarina* have been reported from adjoining regions in the provinces of Chiriquí and Bocas del Toro at 870 to 1,400 m elevation.

Probably related to the lower elevation inhabitant, *Columnea nicaraguensis*, *C. canarina* differs in having yellow flowers rather than red, red maculate leaves vs. all green, and rather than a pendent habit, the plants are more upright herbs or subshrubs.

BOCAS DEL TORO: Trocha 3 de Noviembre, Los Gutiérrez, 870 m, *Dressler 5565* (Dressler coll.).

9. **Columnea cerropirrana** (Wiehl.) L. Skog, comb. nov.

Trichantha cerropirrana Wiehl., Selbyana 2: 129, *pl. 36B*. 1977. TYPE: Panamá, *Duke & Elias 13834* (MO, holotype).

Epiphytic *subshrubs* or vinelike *herbs*; stems spreading, pendent, or climbing by adventitious roots at the nodes, 1–2 mm long, ca. 6 mm in diam., reddish brown, sericeous; branches few. *Leaves* unequal in a pair, the larger leaves elliptic to subfalcate, 6.1–8.8 cm long, 2.4–3.2 cm wide, the apex acuminate, the base oblique, entire, above green, sparsely strigose, below reddish purple, sparsely strigillose to gabrous; petiole 3–6 mm long; smaller leaves ca. 4 cm long, 2 cm wide. *Inflorescences* axillary, of 1(–2) flowers; peduncles lacking; bracts lanceolate, 5 mm long; pedicels ca. 4 cm long, reddish, sericeous. *Flowers* with the calyx lobes nearly equal, lanceolate, 1.2–1.5 cm long, 6–8 mm wide, the apex acuminate, the margin strongly serrate on each side, red, sericeous at the base; corolla red with a yellow limb, the tube erect in the calyx, slightly gibbous at the base, slightly ventricose at the middle, and barely narrowed toward the limb, 2.8–3.8 cm long, sericeous outside, the inside glandular, the lobes of the limb nearly equal, erect, narrowly triangular, 5–8 mm long, the 2 apical lobes connate for a short distance; stamens included, the filaments 7–15 mm long, glabrous, the anthers oblong, free; disc reduced to a bilobed posterior glabrous gland; ovary ovoid, sericeous, the style ca. 1.5 cm long, glabrous; stigma stomatomorphic. Mature *fruit* not seen.

Only two collections of this species are known, both from Cerro Pirre in Darién Province.

DARIÉN: Cerro Pirre, cloud forest and/or mossy forest, 2500–4500 ft, *Duke & Elias 13834* (MO). Cerro Pirre, valley between Pirre and next most southerly peak, sloping hillside, *Folsom 4411* (MO).

10. **Columnea consanguinea** Hanst., Linnaea 34: 384. 1865. TYPE: Turrialva, Costa Rica, *Wendland 509* (not seen).

Dalbergaria consanguinea (Hanst.) Wiehl., Phytologia 27: 317. 1973.

10a. **Columnea consanguinea** Hanst. var. **adpressa** Morley, Ann. Missouri Bot. Gard. 60: 451. 1973. TYPE: Panamá, *Allen 4788* (US, holotype; MO, isotype).

Terrestrial and epiphytic *herbs* or *subshrubs*; stems woody at the base, to 1 m tall, 3–6 mm in diam., pale brown, strigose sericeous. *Leaves* of a pair strongly unequal, the larger leaves lanceolate to oblanceolate, occasionally falcate, 12.2–16.5 cm long and 2.4–5.7 cm wide, membranous to subcoriaceous, the apex acuminate, attenuate and oblique at the base, subentire, dark green above, glabrous, beneath red blotched, strigose, hairs sometimes reddish, 3–6 celled, more numerous on the veins, also 2–3 celled white adpressed hairs; petioles 7–11 mm long, the smaller leaves lanceolate, 1.2–1.8 cm long and 2–6 mm wide, acuminate, oblique at base, green. *Flowers* several in each axil; bracts ovate lanceolate, 9–16 mm long, entire, acute, green, glabrous above; pedicels 2–4 mm long, reddish, coarsely sericeous; calyx lobes lanceolate, 1.5–2.1 cm long, acuminate, entire to subentire, green, strigose; corollas yellow, tubular, 1.6–2.3 cm long and 5 mm in diam. above the base, broader at the middle, slightly contracted at the throat, the lobes subregular, erect, ca. 2 mm long, the outside pale sericeous, the inside glabrous; filaments glabrous, the anthers included; style glabrous, the stigma stomatomorphic. *Fruits* not seen.

This variety is known only from the provinces of Bocas del Toro and Chiriquí in Panamá, but the species also occurs in Costa Rica.

BOCAS DEL TORO: Róbalo Trail, N slopes of Cerro Horqueta, 6000–7000 ft, *Allen 4924* (MO, US). CHIRIQUÍ: Bajo Mono-Róbalo Trail, W slopes of Cerro Horqueta, 5000–7000 ft, *Allen 4788* (MO, US). Bajo Chorro, Boquete District, 6000 ft, *Davidson 57* (MO, US). Cerro Colorado, road along top, 1500–1750 m, *Folsom et al. 4669* (MO, US). NE of Boquete 5 km, 1700–1800 m, *Skog et al. 4043* (MO, US). Bajo Chorro near Río Caldera, 1900 m, *Skog et al. 4057* (MO, US), *4066* (E, MO, PMA, US); *Skog & D'Arcy 4089* (MO, P, US). SW slopes of Cerro Horqueta ca. 6 km NW of Boquete, 1700–1800 m, *Wilbur et al. 15442* (DUKE). Bajo Chorro, 1900 m, *Woodson & Schery 651* (MO).

10b. **Columnea consanguinea** Hanst. var. **darienensis** (Morton) Morley, Ann. Missouri Bot. Gard. 60: 451. 1973.

C. darienensis Morton, Ann. Missouri Bot. Gard. 29: 46. 1942. TYPE: Panamá, *Pittier 5660* (US, holotype).
Dalbergaria darienensis (Morton) Wiehl., Phytologia 27: 317. 1973.

Terrestrial and epiphytic *herbs* and *shrubs*; stems woody below, 4.5–9.0 mm in diam., brown strigose, the bark sometimes red. *Leaves* of a pair strongly unequal, the larger leaves oblanceolate, 17.7–26.2 cm long and 4.2–5.2 cm wide, acuminate, attenuate and oblique at the base, entire, above dark green, glabrous, below green, lacking red spots, strigose, the hairs brown, 3–6 celled, more numerous on the veins, also few 2–3 celled white adpressed hairs; petioles 9–16 mm long; the smaller leaves lanceolate, 1.4–1.7 cm long and 3–4 mm wide, acuminate, oblique at the base, green. *Flowers* several in each axil; bracts ovate, 1.5–1.9 cm long, acute, entire, orange red, glabrous above; pedicels 1–4 mm long, reddish strigose; calyx lobes lanceolate, 1.6–1.9 cm long, acuminate, slightly serrate, serrations 6–7, red, reddish strigose; corollas yellow to orange scarlet,

tubular, 2.0–2.5 cm long, ca. 4 mm in diam. above the base, becoming ca. 5 mm in diam. at the middle, slightly contracted in the throat, the limb lobes subregular, erect, to ca. 3 mm long, the outside coarsely yellowish sericeous; filaments glabrous, the anthers included; ovary strigose at the apex, the style glabrous. *Fruits* ovoid, orange.

Known only from Panamá from the province of Darién this variety differs in lacking red leaf spots.

DARIÉN: Cerro Pirre, *Bristan 548* (MO, OS); 2500–4500 m, *Duke & Elias E13694* (MO, REED); 1400 m, *Folsom 4346* (MO, US); Cuasí-Caná trail between Cerro Campamiento and La Escalera to "paramo" E of Tres Bocas, *Kirkbride & Duke 1266* (MO, NY, REED). Cerro de Garagará, Sambú basin, S Darién, 500–974 m, *Pittier 5660* (US). Caná-Cuasí Trail, *Terry 1547* (GH, MO).

11. **Columnea crassa** Morton, Ann. Missouri Bot. Gard. 29: 45. 1942. TYPE: Panamá, *Allen 2423* (US, holotype).

Dalbergaria crassa (Morton) Wiehl., Phytologia 27: 317. 1973.

Large *herbs* or small *shrubs*, terrestrial or epiphytic; stems to 1 m tall, 4–10 mm in diam., green to reddish, densely brown hirsute, glabrescent below. *Leaves* of a pair strongly unequal, the larger leaf in a pair oblanceolate, 20.4–21.6 cm long and 4.9–6.5 cm wide, the apex acuminate, attenuate and oblique at the base, entire, above dark green, glabrous, below red spotted toward apex, densely strigose, hairs brown to reddish, 4–7 celled, more numerous on the veins and redder at the margins of the leaf, also few 2–3 celled white adpressed hairs; petioles 5–10 mm long; smaller leaves lanceolate, 2.0–4.1 cm long and 1.1–1.6 cm wide, long acuminate, entire, oblique at the base, green. *Flowers* solitary to several in each axil; bracts ovate, 2.0–3.2 cm long, serrate, acuminate, yellowish green to deep red, hirsute above and notably hirsute on the prominent veins below; pedicels to 3 mm long, coarsely sericeous; calyx lobes ovate, 2.2.–2.5 cm long, acuminate, serrate, serrations 5–10, green or deep red, coarsely sericeous; corollas yellow, tubular, ca. 2.5 cm long, ca. 5 mm in diam. above the base, becoming ca. 6 mm in diam. above, externally coarsely sericeous; lobes subregular, erect, to ca. 2 mm long; anthers included; ovary ovoid, appressed pilose, the style and the stigma not seen. *Fruits* ovoid, 1.4–1.7 cm long, 0.8–1.0 cm in diam. when immature, orange to yellow.

This species is known only from Panamá from the provinces of Coclé, Panamá, and Veraguas.

COCLÉ: Cerro Pilón above El Valle de Antón, *Croat 14351* (MO, NY, USF). Summit of Cerro Pilón above El Valle de Antón, 2700 ft, *Dwyer et al. 4508* (MO). El Valle, end of road leading to Turistico Hotel, *Folsom 3136* (MO). El Copé, El Petroso, Atlantic slope of Alto Calvario, *Folsom & Lantz 1875* (MO, US). La Mesa N of El Valle, 1000 m, *Gentry 6839* (MO, PMA). Cerro Pilón, *Lallathin 5083* (MO). Cerro Pilón, 900–1173 m, *Liesner 785* (MO, NA). Cerro Pilón 5 km NE of El Valle, 800–1045 m, *Mori et al. 6581* (MO). Foot of Cerro Pilón above El Valle de Antón, 2000 ft, *Porter et al. 4457* (MO). La Mesa above El Valle 800 m, *Skog & Butcher 4116* (MO, US). El Petroso at Rivera's sawmill 7 km beyond El Copé, 800 m, *Skog et al. 4198* (E, MO, US). PANAMÁ: Cerro Campana, 1000 m, *Allen 2423* (US). Road to Cartí 7–19 km N of El Llano, 400–900 m, *Busey 900* (US); *Correa et al. 1860* (PMA); *Dressler 4273* (MO, PMA), *4546* (PMA); *Folsom 3567* (MO). Capira, NE side of Cerro

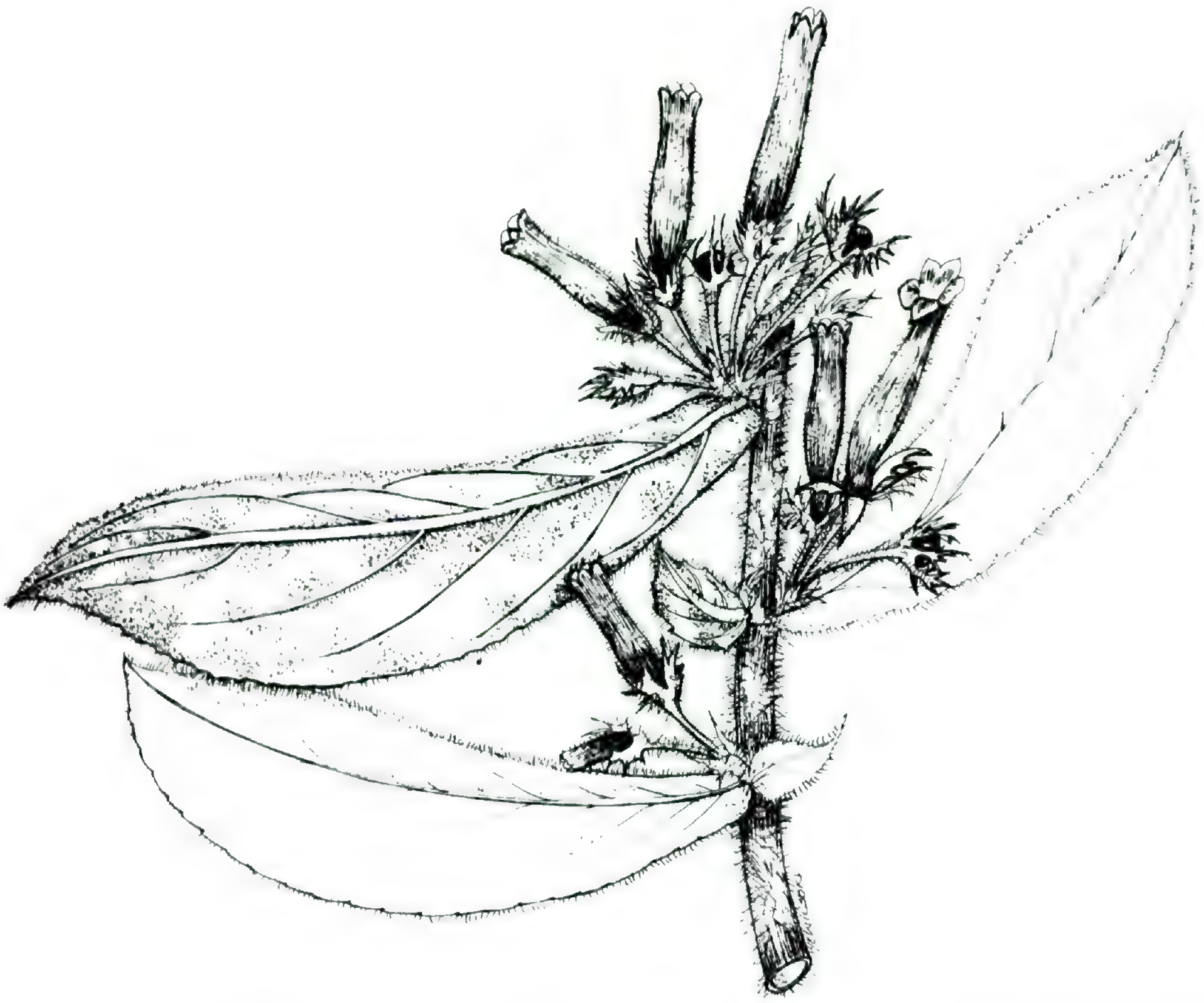

FIGURE 9. *Columnea cruenta* Morley. Flowering branch with flowers (×⅗). [After *Mori & Kallunki 5092* (MO).]

Trinidad, 900 m, *Foster 2113* (DUKE, MO, PMA). 8–17.5 km above Panamerican Highway from El Llano to Cartí-Tupile, *Kennedy et al. 2420* (US); *Liesner 1294* (US); *Mori et al. 4609* (MO); *Nee et al. 8736* (MO). Cerro Campana, 1000 m, *Nee & Stockwell 11624* (MO); *Porter et al. 4281* (MO). Llano-Cartí road, 11.2 km from El Llano and junction with Panamerican Highway, 600 m, *Skog & Folsom 4175* (MO, PMA, US). VERAGUAS: Valley of Río Dos Bocas 11–16.5 km beyond Agriculture School at Santa Fé, 350–550 m, *Croat 25758, 27783* (both MO). Guabal, Río Dos Bocas, 16 km NW of Santa Fé, 500 m, *Dressler 4792, 4793* (both PMA). 6–7 km outside of Santa Fé, *Folsom 2952* (MO, US); *Gentry 2968* (MO); *Nee 11264* (MO).

12. **Columnea cruenta** Morley, Ann. Missouri Bot. Gard. 60: 458. 1973. TYPE: Panamá, *Dwyer et al. 7235* (MO).—FIG. 9.

Dalbergaria cruenta (Morley) Wiehl., Selbyana 2: 102. 1977.

Epiphytic *herbs* or *shrubs*; stems somewhat woody, to 1 m tall, 5–10 mm in diam., purple brown, densely hirsute. *Leaves* of a pair unequal; larger leaf oblanceolate, to 23 cm long and 2.0–5.5 cm wide, acuminate, oblique at the base, the margin serrate toward the apex, green above but suffused purple red near the margins and the tip, pilose, the hairs reddish, 4–5 celled, blotched red purple beneath at the tip, along the margins and towards the center, pilose,

the hairs reddish, 5–6 celled, also 2–3 celled white adpressed hairs; petioles to 6 mm long; the smaller leaves ovate, ca. 1–4 cm long and 6–16 mm wide, acuminate, the margin serrate, vestiture as in larger leaves, leaf tip purple red beneath. *Flowers* 2 or more at a node; bracts not seen; pedicels 9–26 mm long, brown pilose to long villous; calyx lobes lanceolate, 0.9–1.8 cm long, the apex acuminate, 3–7 toothed, the teeth linear, to 3 mm long, green or cream colored, brown pilose; corollas yellow with the lower parts of the lobes red producing a red ring at the limb, funnelform but slightly swollen, 3.9–4.6 cm long, about ca. 3 mm in diam. above base, becoming ca. 7 mm in diam., slightly contracted at the throat to 5.5 mm in diam., the outside brown pilose, the lobes subregular, ca. 6 mm long, spreading; filaments remotely pilose at base, later coiled, yellow, the anthers included, 1 mm long and 1.5 mm wide; disc reduced to a bilobed gland; ovary pilose, the style, ca. 4 cm long, yellow, glabrous, the stigma bilobed to stomatomorphic. *Fruits* cream colored.

This species is known only from Panamá and the province of Panamá.

PANAMÁ: Road to Cartí (San Blas) 19 km N of El Llano, 500 m, *Busey* 895 (MO). Camino a Cerro Campana, 2300 ft, *Correa & Dressler 1022* (PMA). Primary forest, Campo Tres, 3 mi NE of Altos de Pacora, 500–800 m, *Croat 22690* (US). El Llano-Cartí Road, 5–6 mi N of Panamerican Highway at El Llano, 350–375 m, *Croat 34776* (MO). Cerro Jefe, 21 km above Panamerican Highway, 600 m, *Croat 35884* (MO). 19 km N of El Llano, El Llano-Cartí Highway, *Dressler 4279* (MO, PMA). Altos de Pacora, 20–24 km NE of Cerro Azul, *Dressler 5266* (PMA). Summit, Cerro Jefe, 2900 ft, *Dwyer et al. 7235* (MO). 10–22 km N of Panamerican Highway on El Llano to Cartí Road, *Folsom & Collins 1514* (MO, US); *Folsom et al. 1908* (MO, US); *Gentry et al. 8874* (MO, US); *Kennedy et al. 3160* (MO, PMA); *Liesner 1234, 1293* (both US); *Mori et al. 4689* (MO); *Mori & Kallunki 5092* (MO, US); 400–450 m, *Nee & Tyson 10959* (MO). Summit of Cerro Jefe, 23 km from Panamerican Highway, 800 m, *Skog et al. 4162, 4216* (both MO, US).

13. **Columnea dissimilis** Morton, Ann. Missouri Bot. Gard. 29: 47. 1942. TYPE: Panamá, *Allen 2483* (US, holotype; F, GH, MO, NY, isotypes).—FIG. 10.

C. translucens Raymond, Bot. Not. 114: 350, *fig. 4–5*. 1961. TYPE: Cultivated in Montreal Botanical Garden as 2940–59, originally from Panamá, *Raymond* (MTJB, not seen).
Ortholoma dissimile (Morton) Wiehl., Phytologia 27: 321. 1973.
Trichantha dissimilis (Morton) Wiehl., Selbyana 1: 34. 1975.

Epiphytic *herbs* or *subshrubs*; stems to 1 m tall, 2–3 mm in diam., woody toward the base, green to red, red to orange hispid, glandular hairs more or less present. *Leaves* of a pair unequal or subequal; larger blade of the pair elliptic oblong, subfalcate, 4.5–11.4 cm long and 1.7–4.4 cm wide, the apex acuminate, oblique at the base, entire to crenate serrate, membranous, above green appressed hairs sometimes reddish, 5–9 celled, sometimes sparse, below green, hirsute, the hairs often reddish, 5–9 celled, more numerous on the veins, also 2–4 celled glandular hairs; petioles 5–12 mm long; smaller leaves elliptic to ovate, 1.3–4.7 cm long and 0.8–2.2 cm wide, acute to obtuse, oblique to rounded at the base, green, reddish hirsute. *Flowers* 1–3 in each axil; bracts about 3 mm long, linear, acuminate, reddish pilose; pedicels 1.1–2.2 cm long, reddish hirsute; calyx lobes lanceolate, 1.6–3.3 cm long, acute, 1–6 toothed, the teeth to 1 mm long, the lobes green, red or orange, red hirsute; corollas orange or red, tubular, 2.1–3.9 cm long, ca. 4 mm in diam. above the base,

becoming ca. 8 mm in diam. above, not noticeably contracted at the throat, appendages between the lobes sometimes hidden by hairs, externally coarsely red sericeous, internally glabrous, the lobes subregular, erect, ca. 4 mm long, the lobes transparent or yellow sericeous; filaments glabrous, the anthers included; ovary pilose, the style glabrous, the stigma bilobed. *Fruit* white when mature.

Columnea dissimilis is known only from Panamá. *Columnea translucens* is known only in cultivation.

COCLÉ: Hills N of El Valle de Antón, 1000 m, *Allen 2164* (MO, US), *2191* (US). Trail to Las Minas N of El Valle de Antón, 1000 m, *Allen 2483* (F, GH, MO, US). On trail to Cerro Pilón WEPCOR weather site 1 km from top, 900 m, *Correa 49* (DUKE). La Mesa above El Valle, *Croat 13395, 25384* (both MO). Cerro Pilón near El Valle, 700–900 m, *Duke 12072* (MO, REED), *12160* (MO, NY, REED). El Valle, 800–1000 m, *Duke 13190* (MO). Between Cerro Pilón and El Valle de Antón, 700–900 m, *Duke & Dwyer 13967* (MO). Above village of El Valle, *Dwyer 1902* (MO). 8.5 mi from El Valle to La Mesa, *Dwyer 10541* (MO). Cerro Gaital Caracoral, rain forest, 2700–3200 ft, *Dwyer & Correa 8883* (MO). La Mesa at El Valle de Antón, *Folsom & Butcher 2791* (MO). El Copé, El Potroso, Atlantic slope of Alto Calvario, *Folsom & Lantz 1877, 1897* (both MO, US). La Mesa, *Gentry 5643* (MO). 9 km from El Valle Market beyond Sr. Furlong's finca, at end of road, *Kennedy et al. 3211* (MO, PMA). Mountains N of El Valle de Antón, 2500–3000 ft, *Lewis et al. 1786* (MO). Boca del Taobré at confluence Río Coclé del Norte, *Lewis et al. 5488* (DUKE, MICH, MO, NY, SCZ). Cerro Pilón, 5 km NE of El Valle, 800–1045 m, *Mori 6572* (MO); 2000 ft, *Porter et al. 4429* (MO, SCZ), *4440* (MO). La Mesa above El Valle, 800 m, *Skog & Butcher 4119* (MO, P, US). El Petroso at Rivera's sawmill 7 km beyond El Copé, 800 m, *Skog et al. 4204* (E, MO, US). Trailside woods near La Mesa 5 mi N of El Valle, *Wilbur & Luteyn 11733* (DUKE, MO). N rim of El Valle de Antón, near Cerro Turega, 650–700 m, *Woodson & Schery 175* (MO). COLÓN: Santa Rita Ridge, 15 mi E of Colón, 1200 ft, *Butcher* (US); *D'Arcy & D'Arcy 6174* (MO, NY). Santa Rita lumber road, E of Colón, *Dressler 3481* (DUKE, MO, PMA). Near Agua Clara rainfall station, Santa Rita Ridge, *Foster 1747* (DUKE, PMA). Santa Rita Ridge trail beyond end of Santa Rita Ridge Road, 17–35 km from Boyd-Roosevelt Highway, 400–800 m, *Mori & Crosby 6324* (MO). Río Guanche ca. 3 km upriver from bridge on road to Portobelo, 25 m, *Mori & Kallunki 5211* (MO, US). PANAMÁ: Above Campana, 600–800 m, *Allen 1875* (GH, MO, US). Road to Cerro Campana, *Croat 14715* (MO). Cerro Campana along trail to summit, *Croat 17205* (MO, NA). Middle slopes of Cerro Campana, ca. 1 mi from Panamerican Highway, 150 m, *Croat 35958* (MO). Ridge between narrow road and peak of Cerro Campana, 800 m, *Foster & Kennedy 2074* (DUKE). Cerro Jefe, Altos de Pacora, trail to Sebastian's house, 18.2 km E of Cerro Azul village (Goofy Lake), 800–900 m, *Gentry & Mori 13418* (MO, US). Cerro Campana, 2600–2800 ft, *Lewis et al. 1923* (MO); *Skog et al. 4145, 4153* (both US); *Smith & Smith 3375* (US); *Witherspoon & Witherspoon 8468* (MO).

14. **Columnea dressleri** Wiehl., Selbyana 2: 98. 1977. TYPE: Cerro Fortuna, Prov. Chiriquí, Panamá, *Dressler 5400* (SEL, holotype, not available for study; Dressler coll., isotype fragment).

Epiphytic or terrestrial *subshrubs*; stems erect or ascending to 45 cm long, strigillose toward the apex, glabrescent below. *Leaves* strongly unequal in a pair; the larger leaves elliptic or oblong, 4.5–10.5 cm long, 1.5–3.0 cm wide, subcoriaceous, the apex acuminate, the base acute, oblique, the margin subentire, ciliate, above dark green, glabrous, below lighter green, sparsely sericeous, the

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FIGURE 10. *Columnea dissimilis* Morton. Habit (×9/10). [After *Skog et al. 4204* (US).]

veins prominent; petioles 0–4 mm long, sericeous; smaller leaves much reduced, often caducous. *Inflorescences* of 1–3 flowers in an axillary cyme; peduncles lacking; bracts small, lanceolate; pedicels to 1 cm long, reddish, sericeous with whitish hairs. *Flowers* showy; calyx lobes free nearly to the base, nearly equal, lanceolate to ovate, 1.2–1.8 cm long, 5–8 mm wide, acuminate, deeply serrate to laciniate, green, or suffused with red, or red maculate near the midvein, sericeous; corolla bright red, yellow or white at the sinuses of the lower lobe, the tube erect in the calyx, curved, ca. 7.5 cm long, with a short spur, the outside pilose with long reddish hairs and mixed with shorter hairs, inside glandular, galea 1.0–1.5 cm long, 2.0–2.3 cm wide, the lateral lobes ca. 8 mm long and wide, the basal lobe oblong, reflexed, ca. 2 cm long; stamens with filaments slender, ca. 6 cm long, reddish, glabrous, the anthers oblong, ca. 4 mm long, coherent apically into 2 pairs; disc reduced to a bilobed dorsal gland; ovary pilose, the style ca. 6.5 cm long, pilose above, the stigma bilobed. *Berry* subglobose, ca. 1.5 cm in diam.; seeds fusiform, ca. 1 mm long, striate.

Columnea dressleri is found in the cloud forests of Chiriquí and Veraguas at upper elevations.

CHIRIQUÍ: Cerro Fortuna, 1200–1400 m, *Dressler 5400* (Dressler coll.). N of San Félix at Chiriquí-Bocas del Toro border, on Cerro Colorado copper mine road along continental divide, 5000–5500 ft, *Mori & Kallunki 5854* (MO, US). VERAGUAS: 6.4 km outside of Santa Fé, *Folsom 2971* (MO). Cerro Tute, ca. 10 km NW of Santa Fé, ridgetop above 1000 ft, *Mori 6742* (MO).

15. **Columnea flaccida** Seem., Bot. Voy. Herald, 186. 1854. TYPE: Woods near Gualaca, Prov. Chiriquí, Panamá, *Seemann 1163* (K, holotype, photo US; BM, isotype, photo MO, NY).

Epiphytic *herbs*; stems pendent, elongate, slender, 2–2.5 mm in diam., reddish strigose. *Leaves* of a pair subequal; blades narrowly oblong to lanceolate, 2.3–3.5 cm long and 7–9 mm wide, the apex acute to acuminate, rounded at the base, entire, above green, sparsely strigose, hairs reddish, 5–6 celled, also 2–3 celled white adpressed hairs, below green, sparsely strigose, hairs reddish, 5–6 celled, 2–3 celled white adpressed hairs especially on the veins; petioles 1–2 mm long. *Flowers* solitary; bracts linear, 2 mm long; pedicels 5–7 mm long, brownish red hirsute; calyx lobes laciniately 4–5 toothed, the teeth to 3 mm long, the lobes 9–12 mm long, red or reddish, red hirsute; corollas scarlet or rose, funnelform, but strongly zygomorphic, 6.1–6.8 cm long, ca. 3 mm in diam. above the base, becoming ca. 9 mm in diam. at the throat, the outside reddish pilose, the limb 2.0–2.6 cm long, the lobes strongly unequal, the posterior pair connate, slightly apiculate at the apex, 1.3–1.5 cm long, the anterior lobe 1.0–1.3 cm long, reflexed; filaments red, glabrous, the anthers exserted; ovary sericeous, the style red, pilose glandular, the stigma bilobed. *Fruits* not seen. *Chromosomes* $2n = 18$ (Lee and Grear, 1963).

Most specimens of this uncommon species have only flowers, with few leaves.

CHIRIQUÍ: Above Cerro Punta, 8000 ft, *Butcher* (PMA). San Vicente on the Río Mula, 2000 ft, *Butcher* (US). Woods near Gualaca, *Seemann 1163* (BM, K).

16. **Columnea florida** Morton, J. Wash. Acad. Sci. 27: 310. 1937. TYPE: Vicinity of El General, Prov. San José, Costa Rica, *Skutch 2436* (US, holotype; GH, K, MO, isotypes).—FIG. 11.

Dalbergaria florida (Morton) Wiehl., Phytologia 27: 317. 1973.

Epiphytic or terrestrial *herbs* or *shrubs*; stems woody nearly to the apex, erect, to 1 m tall, 6–10 mm in diam., brown or scaly and purplish, densely brown hirsute when young. *Leaves* of a pair strongly unequal; larger leaf oblanceolate, 26.0–36.1 cm long and 3.6–11.2 cm wide, the apex shortly acuminate, oblique at the base, entire to denticulate, above green, glabrous, below green with red patches and more or less adpressed pilose, the hairs reddish or brown, 4–10 celled, more numerous on the veins, also 2–3 celled white appressed hairs; petioles 3–17 mm long; smaller leaves lanceolate, 1.2–2.8 cm long and 2–5 mm wide, acuminate, oblique at the base, green. *Flowers* several in each axil; bracts, lanceolate, 7–8 mm long, entire, acute, olive yellow, hirsute; pedicels 2–4 mm long, dark reddish brown hirsute; calyx lobes pectinate, 1.3–2.0 cm long, green, dark brown hirsute (dried), yellow hirsute (fresh), the margin 6–11 toothed, the teeth to 6 mm long; corollas yellow to orange, tubular, ca. 3.4 cm long and 5 mm in diam. above the base, becoming ca. 8 mm in diam. at the middle, slightly contracted at the throat, the outside densely sericeous, the lobes subregular, erect, to ca. 3 mm long; filaments pubescent, the anthers included; ovary pilose, the style pubescent, the stigma bilobed. *Fruit* globose, 1.3 cm long and 9 mm in diam., yellow; seeds fusiform, ca. 1.2 mm long, striate, dark reddish brown.

This species is known from Costa Rica, and from the provinces of Chiriquí, Darién, and Panamá in Panamá.

The attraction of hummingbirds to the red leaf spots on this species was studied by Jones and Rich (1972) in Costa Rica. They found that the leaf spots serve as visual cues to attract the pollinators to the plants rather than floral characters being the prime attractants. This mode of attraction probably occurs in other species of *Columnea* with red leaf spots and non-red or inconspicous flowers.

CHIRIQUÍ: 1 mi E of Cañas Gordas, near Costa Rican border on road to Volcán, 800–1200 m, *Liesner 270* (MO). DARIÉN: Cerro Pirre, *Bristan 545* (MO). Headwaters of Río Tuquesa, ca. 2 km air distance from continental divide, in vicinity of upper gold mining camp of Tyler Kittredge, *Croat 27171* (MO). W slope of Cerro Pirre, 3250 ft, *Duke 6593* (MO). Elfin forest, Cerro Campamiento S of Cerro Pirre, *Duke 15658* (US), *15721* (US). Summit of Cerro Pirre, 1000–1400 m, *Gentry & Clewell 6966* (FSU, MO). Cerro Pirre, 1400 m, *Folsom 4342, 4546* (both MO). Top of Cerro Mali, 1300–1420 m, *Gentry & Mori 13621* (MO, PMA). Cerro de Garagará, Sambú basin, 500–974 m, *Pittier 5664* (US). N slope Caná-Cuasí Trail, *Terry & Terry 1593* (GH). PANAMÁ: Road to Cartí 13 km N of El Llano, 350 m, *Busey 379* (MO). El Llano-Cartí road 10 mi from Panamerican Highway near El Llano, 330 m, *Croat 33753* (MO). La Eneida, region of Cerro Jefe, *Dressler 3316* (MO), *4145* (MO, US). El Llano-Cartí highway, 12–17 km N of El Llano, *Dressler 4545* (PMA). Cerro Jefe on top near antenna, 4000 ft, *Folsom & Harp 1360* (MO, US). Top of Cerro Jefe, *Gentry 2871* (MO, PMA). Cerro Jefe, 16–20 km E of Cerro Azul village, 800–1000 m, *Gentry & Mori 13436* (MO, US). Campo Tres, 3 mi NE of Altos de Pacora, 500–800 m, *Liesner 530* (MO). El Llano-Cartí road, 12 mi above Pan American Highway, 200–500 m, *Liesner 1254* (MO). Gorgas Memorial Labs Yellow Fever research camp, ca. 25 km NE of Cerro Azul on Río Piedras, 550 m, *Mori et al. 3434* (MO). Cerro Jefe, along trail on ridge running NE from summit, 1000 m, *Mori et al. 3732* (MO). El Llano-Cartí Road, 10.8 km from Panamerican Highway, 1100–1200 ft, *Mori*

FIGURE 11. *Columnea florida* Morton. Habit (×⅜). [After *Skog et al. 4218* (US).]

et al. 4117 (MO). El Llano-Cartí Road, 16 km N of Panamerican Highway at El Llano, 400–450 m, *Nee & Dressler 9353* (MO). Summit of Cerro Jefe, 23 km from Panamerican Highway, 800 m, *Skog et al. 4218* (E, MO, P, PMA, US). Cerro Jefe, 2700–3000 ft, *Tyson et al. 3227* (SCZ).

17. **Columnea gallicauda** Wiehl., Selbyana 2: 99. 1977. TYPE: 12–15 km NW of Santa Fé between third branch of Río Santa María and continental divide, *Dressler 5000* (SEL, holotype, not available for study; Dressler coll., isotype).

Epiphytic *subshrubs*; stem erect or ascending, to 40 cm or more long, near the apex sericeous, below glabrescent. *Leaves* strongly unequal in a pair, the larger leaf narrowly lanceolate, falcate, 21–28 cm long, 2–3 cm wide, membranous, the apex long attenuate, the base acute, oblique, the margin entire, above dark green, glabrous, below lighter green, but reddish at the apex, strigillose along the veins; petiole short; smaller leaf minute, caducous. *Inflorescences* axillary, of 1–3 flowers in a reduced cyme; peduncles lacking; bracts ovate, ca. 7 mm long, green and reddish; pedicel 5–9 mm long, green, sericeous. *Flowers* showy; calyx lobes nearly equal, distinct nearly to the base, lanceolate, 2.5–4.0 cm long, long acuminate, laciniate, reddish, sericeous; corolla orange with purple longitudinal stripes, erect in the calyx, the tube curved, ca. 7 cm long with a short spur, outside long pilose mixed with shorter hairs, the inside glabrous, galea ca. 1.2 cm long, 1.5 cm wide, apiculate, the lateral lobes triangular, ca. 5 mm long and wide, the lower lobe linear, to 2 cm long; stamens reaching almost to the limit of the galea, the filaments slender, curved, ca. 6.5 cm long, adnate to the base of the corolla for ca. 7 mm, glandular, the anthers coherent in 2 pairs by their apices; disc reduced to a white bilobed dorsal gland; ovary sericeous, the style ca. 6.5 cm long, the stigma bilobed. *Berry* subglobose, ca. 1.7 cm in diam., white; seeds fusiform, ca. 1 mm long, striate, light brown.

Columnea gallicauda is known only from the province of Veraguas in lower montane wet forest at ca. 900 m. The plants are distinctive by the long attenuate leaves with red tips and the purplish laciniate calyx lobes.

VERAGUAS: Between third branch of Río Santa María and continental divide, 12–15 km NW of Santa Fé, 650–800 m, *Dressler 5000* (Dressler coll.). Lower montane wet forest 7 km W of Santa Fé on new road past agricultural school, along Quebrada Mulaba, a rocky tributary of Río Santa María, 2900 ft, *Nee 11222* (MO, US), *11255* (MO).

18. **Columnea hiantiflora** Wiehl., Selbyana 2: 100, *pl. 29D*. 1977. TYPE: Near Valle Hornito and Cerro Hornito, Fortuna Dam site, Prov. Chiriquí, Panamá, *Dressler 5443* (SEL, holotype, not available for study).

Epiphytic *herbs* or *subshrubs*; stems erect, ascending or spreading, to 40 cm long, 4–6 mm in diam., green, sericeous, becoming tawny. *Leaves* nearly equal in a pair, narrowly elliptic, 5.5–8.5 cm long, 1.0–2.2 cm wide, the apex acute to acuminate, the base cuneate or decurrent into the petiole, nearly entire, above and below green, occasionally pink on the veins, sericeous; petioles 3–9 mm long, sericeous. *Inflorescences* axillary, single flowered; peduncles lacking; bracts linear, ca. 6 mm long, sericeous; pedicels ca. 1 cm long, green, sericeous. *Flowers*

showy, the calyx lobes nearly equal, lanceolate, 1.5–1.9 cm long, acuminate, serrate to laciniate with 5 or 6 teeth, each ca. 3 mm long, outside green, sericeous, the inside glabrous; corolla red, the sinuses of the lobes and throat streaked yellow, the tube erect in the calyx, ca. 7.5 cm long, gibbous at the base, ampliate toward the limb, the outside sparsely pilose, the inside glandular, the limb suberect, galea truncate, 1.6 cm long, ca. 2.2 cm wide, the lateral lobes triangular, ca. 1.2 cm long, the basal lobe oblong, ca. 1.8 cm long, 1 cm wide; stamens reaching the galea, the filaments curved, 5.5 cm long, adnate to the corolla tube base for ca. 1 mm, reddish, glandular pubescent, the anthers oblong, ca. 3 mm long; disc reduced to a bilobed posterior white gland; ovary sericeous, the style ca. 6.5 cm long, glandular pilose, the stigma stomatomorphic to bilobed. *Fruits* not seen.

According to the discussion with original description, the wide-mouthed corollas of *Columnea hiantiflora* resemble those of *C. incarnata*, also from the province of Chiriquí, but the plants of the latter species differ in having larger, nearly entire, glabrous calyx lobes.

From the original description and illustration, *Columnea hiantiflora* seems to greatly resemble *C. magnifica*, so far not definitely known from Panamá, but common in Costa Rica at similar elevations and in similar habitats. *Columnea magnifica* differs primarily in having oblanceolate leaves and less deeply toothed calyx lobes. *C. hiantiflora* may be a variant of the common Costa Rican species.

CHIRIQUÍ: Camp Hornitos (Fortuna dam site), 82°10′W, 8°44′N, 1100–1200 m, *Dressler 5445* (Dressler coll.).

19. **Columnea hirsutissima** Morton, Ann. Missouri Bot. Gard. 29: 47. 1942. TYPE: Panamá, *Allen* 2288 (US).—FIG. 12.

Epiphytic *herbs* or *subshrubs*; stems woody at the base, 3–6 mm in diam., green when young, brown or reddish hirsute. *Leaves* of a pair strongly unequal; larger leaf oblong, 5.5–10 cm long and 1.9–3.0 cm wide, membranous to fleshy, the apex acute to shortly acuminate, rounded or subcordate at the base, more or less serrate, above green and densely hirsute, the hairs reddish or transparent, 4–13 celled, also a few 2–3 celled white adpressed hairs, below green to purplish, densely hirsute, the hairs brownish, transparent or reddish, 4–13 celled, more numerous on the veins; petioles 1–4 mm long; smaller leaves ovate, 1.4–3.9 cm long and 6–14 mm wide, acute, sessile, green, apparently soon caducous. *Flowers* 2–3 in each axil; bracts linear, 2–4 mm long, reddish hirsute; pedicels 8–14 cm long, reddish to brown hirsute; calyx lobes linear, erect, 1.5–2.3 cm long, the apex long acuminate, entire or remotely toothed, the teeth 2–4, 1 mm long at most, the lobes green or red, long reddish or brown hirsute; corollas scarlet or rose with yellow or white stripes running along the anterior side of the tube, funnelform but strongly zygomorphic, 5.6–6.8 cm long, ca. 4 mm in diam. above the base, becoming ca. 9 mm at the throat, externally long reddish pilose, internally short pilose, the lobed portion of the corolla, 2.1–2.9 cm long, the lobes strongly unequal, the posterior pair connate, truncate at the apex, 8–11 mm long, the anterior lobe, 1.2–1.8 cm long, reflexed; filaments yellow, glabrous

FIGURE 12. *Columnea hirsutissima* Morton. Habit (×1). [After *Skog & Butcher 4128* (US).]

above, the anthers exserted; ovary pilose, the style yellow, glandular pilose, the stigma stomatomorphic. *Fruits* ovoid, ca. 7 mm in diam., white. *Chromosomes* $2n = 18$ (Lee, 1967).

Columnea hirsutissima is known only from Panamá, from the provinces of

Chiriquí, Coclé, Panamá and Veraguas. Leaf and flower color forms have been named as cultivars.

CHIRIQUÍ: Cerro Otoe, 15–20 km N of San Félix, 3000 ft, *Bort 19* (MO). COCLÉ: Hills N of El Valle de Antón, 800–1000 m, *Allen 2279* (US, US), *2288* (US), *2311* (US), *2348* (US). N of El Valle de Antón, La Mesa, 1000 m, *Allen 2792* (US). N of El Valle de Antón on trail to Las Minas, 1000 m, *Allen 2882* (GH, MO, MO, US). Hills N of El Valle de Antón, *Dressler 5291* (PMA). La Mesa to El Valle, 2000–2500 ft, *Duke & Dwyer 8265* (MO). Cerro Pilón, El Valle, 3000 ft, *Duke & Lallathin 15013* (MO, PMA). La Mesa above El Valle, *Dwyer & Nee 11929* (MO). Aseradera Rivera, Alto de Calvario, 7 km N of El Copé, 700 m, *Folsom 2324* (MO). Rivera's sawmill, Alto Calvario, *Folsom 3171* (MO, US), *3250* (MO). Hills above El Valle, 1000 m, *Gentry 6880* (MO). 5 mi N of El Valle near Furlong's house, *Gentry & Dwyer 3629* (MO). Foot of Cerro Pilón, 2500 ft, *Gentry & Dwyer 3641* (F). Mountains beyond La Pintada, 400–600 m, *Hunter & Allen 553* (MO, US). El Valle de Antón, 1000–2000 ft, *Lewis et al. 2531* (MO). Cerro Pilón, 900–1173 m, *Liesner 762* (MO). La Mesa 4 km N of El Valle, 875 m, *Nee & Dwyer 9177* (MO). La Mesa 4 km N of El Valle, 875 m, *Nee & Hale 9668* (MO). Foot of Cerro Pilón above El Valle de Antón, 2000 ft, *Porter et al. 4379* (MO). La Mesa above El Valle, 800 m, *Skog & Butcher 4128* (MO, US). La Mesa 3 km N of El Valle de Antón, 850 m, *Wilbur et al. 15623* (DUKE). PANAMÁ: Cerro Jefe, 3000 ft, *Butcher 2* (US); *Gentry et al. 3475* (DUKE, MO, NY); *Mori et al. 3747, 3778* (both MO); 2700–3000 ft, *Tyson et al. 3303* (SCZ). VERAGUAS: From third branch of Río Santa María to continental divide, 12–15 km NW of Santa Fé, 650–800 m, *Dressler 4997* (PMA). Road from Santa Fé past Agricultural School to base of Cerro Tute, 1000–1200 m, *Folsom 1591* (MO, US). Above Santa Fé on slopes of Cerro Tute, 1200–1400 m, *Gentry 6252* (MO). Caribbean slope above Río Primero Brazo 5 mi NW of Santa Fé, *Liesner 1005* (MO). Road beyond Escuela Agricola Alto Piedra above Santa Fé, 800–1000 m, *Luteyn & Wilbur 4567* (DUKE); *Mori & Kallunki 4739* (MO, US), *5334* (MO); *Nee 9789* (MO, US), *11262* (MO).

20. **Columnea hirta** Klotzsch & Hanst., Linnaea 34: 403. 1865. Based on *Columnea hirsuta* Klotzsch ex Oerst.

C. hirsuta Klotzsch ex Oerst., Cent. Gesn. 61. 1858, non Sw. TYPE: "Veragua," *Warscewicz* (not seen).

20a. **Columnea hirta** Klotzsch & Hanst, var. **hirta**

Suffrutescent, epiphytic *herbs*; stems 2.5 mm in diam., red hirsute. *Leaves* of a pair subequal, oblong, 3–4 cm long and 13–17 mm wide, the apex obtuse, rounded at the base, remotely serrate, above green, densely pilose, the hairs transparent, 4–5 celled, below green, densely pilose, the hairs transparent, 4–7 celled, also 2–3 celled transparent adpressed hairs; petioles 4–5 mm long. *Flowers* 1–2 in each axil; bracts linear, ca. 4 mm long; pedicels 6–7 mm long, transparent to reddish hirsute; calyx lobes lanceolate, 12–15 mm long, acuminate, green, transparent hirsute, 2–3 toothed, the teeth to 1 mm long; corolla orange scarlet, funnelform but strongly zygomorphic, 7.0–8.2 cm long, ca. 4 mm in diam. above the base, becoming 12 mm in diam. at the throat, externally red pilose, the lobed portion of the corolla ca. 2.9 cm long, the lobes strongly unequal, the posterior pair connate, truncate and cusped at the apex, ca. 1.8 cm long, the anterior lobe ca. 1.5 cm long, spreading; filaments red, minutely pilose above; ovary hirsute, the style yellow, minutely pilose glandular above, the stigma stomatomorphic. *Fruits* not seen. *Chromosomes* $n = 9$ (Eberle, 1956).

Apart from the type which was destroyed in Berlin, *Columnea hirta* var. *hirta* is not otherwise known from Panamá, although it occurs in neighboring parts of Costa Rica.

20b. **Columnea hirta** Klotzsch & Hanst., var. **mortonii** (Raymond) Morley, Ann. Missouri Bot. Gard. 60: 455. 1973.

C. mortonii Raymond, Bot. Not. 114: 346. 1961. TYPE: Cultivated at the Montreal Botanical Garden, acc. no. 1820–56, believed to be from Panamá originally, *Raymond* (MTJB, holotype, not seen; US, isotype).

Suffrutescent *herbs*, epiphytic; stems 2.5 mm in diam., orange brown hirsute. *Leaves* of a pair subequal; blades suborbicular, ovate or oblong, 1.8–2.4 cm long and 9–12 mm wide, the apex obtuse to acute, rounded to cuneate at the base, the margin subentire, above green and densely pilose, the hairs transparent, 4–5 celled, below green, densely pilose, the hairs transparent, 4–7 celled, also 2–3 celled white adpressed hairs especially on the veins and the margins of the leaf; petioles 3–5 mm long. *Flowers* solitary; bracts linear triangular, 1 mm long; pedicels 2–3 mm long, transparent to orange pilose glandular; calyx lobes lanceolate to oblong linear, 8–11 mm long, acuminate, green or reddish, orange or transparent hirsute, the margin remotely toothed to subentire; corollas orange red, funnel shaped but strongly zygomorphic, 6.5–7.0 cm long, ca. 4 mm in diam. above the base, becoming ca. 12 mm in diam. at the throat, the outside red hirsute, more or less glandular, the lobed portion of corolla 2.7 cm long, the lobes strongly unequal, the posterior pair connate, submucronate, ca. 1.8 cm long, the anterior lobe ca. 1.2 cm long, spreading; filaments red, glandular pilose to minutely pilose; ovary white pilose, the style yellow, more or less glandular, the stigma stomatomorphic. *Fruit* 1.5 cm in diam., white, pilose. *Chromosomes* $2n = 18$ (Lee, 1962).

This taxon is known only in cultivation. Variety *mortonii* may replace var. *hirta* in Panamá if the taxonomic characters separating the two are constant, but on present data there is reason to think that var. *mortonii* is really synonymous with var. *hirta*.

21. **Columnea illepida** Moore, Baileya 8: 56. 1960. TYPE: Cultivated at Cornell University, Ithaca, New York, from plants originally collected at Cerro Jefe, Prov. Panamá, Panamá by H. Butcher, *Moore 7740* (BH, holotype; US, isotype).

Trichantha illepida (Moore) Morton, Contr. U.S. Natl. Herb. 38: 12. 1963.
Ortholoma illepidum (Moore) Wiehl., Phytologia 27: 322. 1973.

Suffrutescent *herbs*; stems 4 mm in diam. (8–9 mm in cultivation), yellowish hirsute. *Leaves* of a pair strongly unequal; larger leaf lanceolate to oblanceolate, 6.9–12.5 cm long and 2.5–5.1 cm wide, the apex abruptly acute acuminate, oblique at the base, denticulate, above green, hirsute, hairs transparent or reddish especially near the margins of the leaf, 6–9 celled, below red blotched or red concolorous, hirsute, the hairs transparent or reddish, 5–7 celled, more numerous on the veins, also 2–3 celled white adpressed hairs; petioles 4–21 mm long; smaller leaves ovate lanceolate, acute, ca. 1.0 cm long and 5 mm wide, caducous. *Flowers* solitary or several in each axil; bracts linear, ca. 2 mm long, hirsute; pedicels ca. 1.8 cm long, transparent hirsute; calyx lobes 3–5 toothed, the teeth 2 mm long, the lobes, 1.4–1.8 cm long, green, transparent hirsute; corollas yellow with dark

red stripes arising from the margins of the lobes, ca. 5.3 cm long, funnel shaped but slightly swollen, the appendages between the lobes 1 mm long, yellow, the tube 3–4 mm in diam. above the base, becoming ca. 10 mm in diam. at the middle, contracted to about 8 mm at the throat, externally sparsely hirsute, the lobed portion of the corolla ca. 9 mm long, the lobes slightly unequal, 2 posterior lobes connate, the anterior lobe ca. 4 mm long; filaments pilose towards the base, the anthers included; ovary pilose, style slightly pubescent, yellow, the stigma bilobed. *Fruits* ovoid, gray white, pubescent.

This species is now known only in cultivation, but is originally from Panamá.

Morton (1971, p. 180) misinterpreted the letter from Henry Butcher, the original finder of *Columnea illepida*, and placed the plant in the province of Chiriquí. On rereading the letter we see that Butcher states that the plant actually "came from Cerro Jefe not too far from where *C. moorei* came from, about 4 miles north of Jefe proper, 3000′ in cloud forest," in the province of Panamá.

CULTIVATED: Cornell University, Ithaca, New York, *Moore 7740* (BH, US). Fantastic Gardens, Miami, Florida, *Wilson* (US).

22. **Columnea incarnata** Morton, Ann. Missouri Bot. Gard. 29: 48. 1942. TYPE: Panamá, *Woodson & Schery 608* (MO, holotype).—FIG. 13.

Ortholoma incarnatum (Morton) Wiehl., Phytologia 27: 322. 1973.
Trichantha incarnata (Morton) Wiehl., Selbyana 1: 35. 1975.

Herbs, epiphytic, suffrutescent or vinelike; stems to 60 cm tall, 6–7 mm in diam., yellowish strigose. *Leaves* of a pair unequal; larger leaf lanceolate to oblanceolate, 9.2–12.7 cm long and 2.2–3.3 cm wide, long acuminate, cuneate at the base, entire, above green, glabrous or sparsely strigose, the hairs white, 2–3 celled, below green or red concolorous, sparsely strigose, the hairs transparent to reddish, 3–8 celled mainly on the veins and along the leaf margin, also few 2–3 celled white adpressed hairs; petioles 2.1–2.3 cm long; smaller leaves lanceolate, 5.8–7.9 cm long and 2.1 cm wide, acuminate, cuneate. *Flowers* solitary or in small clusters; bracts linear, 5–15 mm long, strigose; pedicels 3.8–4.2 cm long, coarsely yellow sericeous; calyx lobes ovate, 3.1–3.8 cm long, the apex long acuminate, remotely denticulate, green, red or becoming reddish with age, sparsely strigose but more so around the margins; corollas scarlet or bright pink, sometimes with traces of white mottling on the margins of the lobes, much dissected, zygomorphic, the tube ventricose but bent, 6.1–6.8 cm long, ca. 5 mm in diam. above the base, becoming 14 mm at the throat, externally red pilose; lobed portion of the corolla 4.5–5.0 cm long, the lobes strongly unequal, the posterior lobes connate, 3.0–3.2 cm long, truncate at the apex, the anterior lobe ca. 3.3 cm long, spreading; filaments red, glabrous, the anthers exserted, 3 mm long, 1 mm wide; ovary sericeous, the style glabrous, the stigma bilobed. *Fruits* not seen.

Columnea incarnata is known only from Panamá, from the provinces of Bocas del Toro and Chiriquí.

FIGURE 13. *Columnea incarnata* Morton. Habit (×7/10). [After *Allen 4948* (MO).]

BOCAS DEL TORO: Róbalo Trail, northern slopes of Cerro Horqueta, 6000–7000 ft, *Allen 4948* (MO, US). CHIRIQUÍ: Above San Félix along mining road 18–27 mi off of Panamerican Highway, 1200–1500 m, *Croat 33042* (MO). Above Río San Félix near San Félix, 800–1200 m, *Croat 33471* (MO). Cerro Colorado, 1500–1750 m, *Folsom et al. 4668* (MO, US). Cerro Horqueta, 5000–7000 ft, *Kirkbride 130* (MO, MO, SCZ). Bajo Chorro, 1900 m, *Woodson & Schery 608* (MO). Cerro Colorado on upper mining road 20–28 mi from San Félix, 1200–1500 m, *Croat 33390* (MO).

23. **Columnea kahlbreyeriana** Masters, Gard. Chron., n. s., 17: 44. 1882. TYPE: Cultivated material originally collected in the forests of Ciñegetas, Prov. Antioquia, Colombia by Kahlbreyer (not seen).

C. kahlbreyeri Hook. f., Bot. Mag. 108: *tab. 6633*. 1882. Based on *Columnea kahlbreyeriana* Masters.

C. citrina Morton, Ann. Missouri Bot. Gard. 29: 44. 1942. TYPE: Panamá, *Allen 2404* (US, holotype).

C. conferta Morton, Ann. Missouri Bot. Gard. 29: 44. 1942. TYPE: Panamá, *Terry & Terry 1554* (F, holotype; GH, isotype).

Dalbergaria kahlbreyeriana (Masters) Wiehl., Phytologia 27: 318. 1973.

Suffrutescent *herbs* or *shrubs*, terrestrial and epiphytic; stems to 1 m long, 4–8 mm in diam., transparent strigose. *Leaves* of a pair strongly unequal; larger leaf narrowly oblong, 20.1–27.7 cm long and 4.3–4.9 cm wide, long acuminate, strongly oblique at the base, serrate, green above, glabrous, below green or red spotted, strigose, the hairs transparent, 4–10 celled, fine, also 2–3 celled white appressed hairs; petioles lacking or to 2 mm long; smaller leaves lanceolate, 1.2–1.7 cm long and 4 mm wide, acuminate, oblique at the base, green. *Flowers* in pairs; bracts lanceolate, 1.4–1.5 cm long, pale brown hirsute; pedicels 1.1–1.8 cm long, transparent to brown strigose; calyx lobes ovate, 2.8–3.4 cm long, the apex long acuminate, coarsely dentate, greenish yellow, sparsely strigose; corollas yellow with pink or red stripes, funnel shaped but strongly zygomorphic, 5.1–6.1 cm long, ca. 6 mm in diam. above the base, becoming ca. 8 mm at the throat, outside reddish hirsute, the lobed portion of the corolla 2.9–3.6 cm long, the lobes strongly unequal, the posterior pair connate, bilobed at the apex, ca. 1.1 cm long, the anterior lobe 2.1–2.8 cm long, reflexed; filaments yellow, glabrous, the anthers exserted; ovary sericeous, the style glabrous, yellow, the stigma stomatomorphic. *Fruits* not seen.

This species is known from Colombia, and from Panamá in the provinces of Coclé, Darién, Panamá, and Veraguas.

COCLÉ: Hills N of El Valle de Antón, *Dressler 2950* (US). Cerro Pilón, 900–1173 m, *Liesner 761* (MO). DARIÉN: Cerro Campamiento, S of Cerro Pirre, *Duke 15606* (US), *15607* (US). Crest of Caná-Cuasí Trail, Chepigana District, 1650 m, *Terry & Terry 1554* (F, GH). PANAMÁ: Cerro Campana, 1000 m, *Allen 2404* (US); 2600–2800 ft, *Lewis et al. 1917* (MO); 850 m, *Liesner 608* (MO). VERAGUAS: 0.6 mi beyond Escuela Agricola Alto Piedra, 730 m, *Croat & Folsom 34021A* (MO). 15–20 km NW of Santa Fé between Escuela Agricola Alto Piedra and continental divide, 650–800 m, *Dressler 4734* (PMA).

24. **Columnea maculata** Morton, Proc. Biol. Soc. Washington 69: 194. 1956. TYPE: Panamá, *Wedel 2280* (US, holotype; US, isotype).

Epiphytic *shrubs*; stems woody, to 8 mm or more in diam., yellowish ginger pilose. *Leaves* of a pair strongly unequal; larger leaf oblong oblanceolate, to 23 cm long and 8.7 cm wide, acute, oblique at base, entire, above green, pilose, the hairs transparent, 7–8 celled, suffused pink beneath with deeper red tip, pilose, the hairs transparent or reddish, more numerous on the veins, 5–8 celled, also 2–3 celled white appressed hairs; petioles ca. 2 mm long; smaller leaves not seen. *Flowers* solitary; bracts ca. 5 mm long; pedicels ca. 3 mm long, gingery pilose; calyx lobes ovate lanceolate, ca 1.7 cm long, the apex long acuminate, laciniately toothed, the teeth to 2 mm long, the lobes green or pinkish to dark red, gingery pilose; corolla greenish yellow or yellow with red to black striping and spotting, funnel shaped but strongly zygomorphic, ca. 7.1 cm long and 4 mm in diam. above the base, becoming ca. 7 mm in diam. at throat, externally pale yellow pilose to sericeous, the lobed portion of the corolla ca. 3.3 cm long, the lobes strongly unequal, the posterior pair connate, bilobed at the apex ca. 1.7 cm long, the anterior lobe ca. 2.1 cm long, reflexed; filaments reddish, minutely pilose glandular, the anthers exserted; ovary sericeous, the style yellow, minutely pilose glandular, the stigma stomatomorphic. *Fruits* white.

This species is known only from Panamá, from the provinces of Bocas del Toro, Chiriquí, Coclé, Panamá, and Veraguas.

BOCAS DEL TORO: Fish Creek Mountains, Chiriquí Lagoon, *Wedel 2280* (US, US). CHIRIQUÍ: Camp Hornitos, Fortuna dam site, 82°10′W, 8°44′N, 1000–1200 m, *Dressler 5422* (PMA). COCLÉ: Atlantic slope of mountain 7 km N of El Copé, Alto Calvario, *Folsom 1249* (US). PANAMÁ: 4.8 mi N of Panamerican Highway just W of El Llano, *Gentry 5098* (MO). VERAGUAS: Caribbean slope above Río Primero Brazo 5 mi NW of Santa Fé below Escuela Agricola Alto Piedra, 700–1200 m, *Croat 23246* (MO). 0.2 mi beyond fork in road at Escuela Agricola Alto Piedra on road to Río Calovébora, 750 m, *Croat & Folsom 33880* (MO). Buabal, Río Dos Bocas about 16 km NW of Santa Fé, 500 m, *Dressler 4773* (PMA). Mountains 3–5 mi N of Santa Fé, 500–1000 m, *Gentry 2963* (MO, NY, PMA), *3025* (F, MO). Cerro Tute, 10 km W of Santa Fé, above 1000 m, *Mori 6289* (MO). 6–7 km W of Santa Fé on new road past agriculture school, 2900 ft, *Nee 9726* (MO, US).

25. **Columnea magnifica** Klotzsch ex Oerst., Cent. Gesn. 60. 1858. TYPE: Costa Rica, *Warscewicz* (C, holotype; MO, US, photo).

C. wendlandiana Hanst., Linnaea 34: 402. 1865. TYPE: Costa Rica, *Wendland 1270* (not seen).

C. oblanceolata Sprague, Bull. Misc. Inform. 1908: 449. 1908. TYPE: Costa Rica, *Hübsch* (K, US, not seen).

Suffrutescent epiphytic *herbs*; stems 4 mm in diam., pale brown hirsute. *Leaves* of a pair subequal, obovate to narrowly oblanceolate, 3.1–6.8 cm long and 1.0–2.8 cm wide, the apex acute, cuneate to rounded at the base, entire, above green, more or less pilose, the hairs transparent, 4–8 celled, green or suffused red beneath, pilose, hairs transparent or reddish, 4–8 celled, also 2–3 celled white hairs and few glandular hairs; petioles 1.0–1.6 cm long. *Flowers* 1–3 in each axil; bracts linear, 4 mm long, pilose; pedicels 1.0–1.8 cm long, pale brown or red pilose; calyx lobes ovate lanceolate, 1.4 cm long, acuminate, 4–5 toothed, the teeth ca. 2 mm long, green with red streaks, hirsute; corollas scarlet with the lobes edged yellow or with yellow areas running from the sinuses of the anterior lobe to the base of the corolla, strongly zygomorphic, the tube ventricose but bent, 6.5–6.7 cm long, ca. 4 mm in diam. above the base, becoming ca. 15 mm in diam. at the throat, red pilose, the lobed portion of the corolla, 3.2–3.9 cm long, the lobes strongly unequal, the posterior lobes connate, 2.0–2.5 cm long, entire at the apex, the anterior lobe ca. 2.0 cm long, spreading; filaments yellow, minutely pilose, the anthers exserted; ovary pilose, the style reddish, minutely pilose glandular, the stigma bilobed. *Fruits* not seen. *Chromosomes* $2n = 18$ (Lee, 1966a).

Since the species is known in neighboring regions in Costa Rica, *Columnea magnifica* is likely to occur in Panamá. In fact, *C. hiantiflora* may be a variant of this species in Panamá.

26. **Columnea microcalyx** Hanst., Linnaea 34: 408. 1865. TYPE: Costa Rica, *Wendland 910* (B, not seen, no longer extant).

C. microcalyx var. *macrophylla* J. D. Smith, Bot. Gaz. (Crawfordsville) 31: 118. 1901. TYPE: Forests near Las Vueltas, Tucurrique, Costa Rica, *Tonduz 12932* (US, isotype).

C. tuerckheimii Sprague, Bull. Misc. Inform. 1912: 42. 1912. TYPE: Cubilquitz, Dept. Alta Verapaz, Guatemala, *Tuerckheim* in J. D. Smith *7640* (US, isotype).

C. lutea J. D. Smith, Bot. Gaz. (Crawfordsville) 57: 425. 1914. TYPE: Cubilquitz, Dept. Alta Verapaz, Guatemala, *Tuerckheim* in J. D. Smith 7930 (US, holotype).
C. localis Morton, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1165. 1938. TYPE: Based on *Columnea microcalyx* var. *macrophylla* J. D. Smith, not *C. macrophylla* Kuntze.

Epiphytic or rarely trailing woody-based *herbs*; stems pendent, slender, to 2 m long, ca. 1–3 mm in diam., branched, strigose hirsute with reddish or transparent hairs, becoming gray brown with age. *Leaves* subequal in a pair; ovate elliptic, 1.2–3.2 cm long, 5–13 mm wide, the young leaves thin, becoming thicker and reddish with age, the apex acute, rounded to cordate at the base, subentire to serrulate, occasionally reflexed, adaxially green, sparsely strigose to densely pilose, occasionally with reddish hairs, abaxially dark green with reddish or transparent hairs, densely pilose especially on the prominent veins; petioles 1–2 mm long, pilose. *Inflorescences* axillary, single flowered; bracts 1–2 mm long, pilose; pedicels 0.9–3.7 cm long, hirsute to pilose with reddish or transparent hairs. *Flowers* showy; calyx spreading, the lobes oblanceolate, 1.0–1.2 cm long, acute or obtuse at the apex, the margin entire to remotely serrulate, green or reddish, hirsute; corolla pink, orange red to deep purple, with or without yellow areas on the lower side, the tube funnel shaped, strongly zygomorphic, 6–7 cm long, the tube gibbous at the base, ca. 3 mm wide, becoming 10–11 mm wide at the throat, the lobed portion of the corolla 4.3–5.1 cm long, the lobes strongly unequal, the upper lobes truncate at the apex 1.0–1.9 cm long, the lower lobe reflexed, ca. 3 cm long, the outside reddish pilose, the inside glandular; stamens exserted, the filaments reddish, glabrous, the anthers coherent; ovary villous, the style yellow pilose, the stigma bilobed. *Berry* globose, ca. 1 cm in diam., at first white or transparent, becoming nearly black from the dark colored seeds within, surrounded by the persistent calyx.

Columnea microcalyx is known from Guatemala and Costa Rica, through Panamá into northern South America. In Panamá, specimens have been collected from the provinces of Chiriquí, Coclé, Darién, and Veraguas in wet forests at upper elevations.

The plants included here have borne a variety of names, more recently confused because of the loss of the holotype of *Columnea microcalyx* which was probably at Berlin (B). Until a neotype is selected the taxon must rest on the description given by Hanstein.

The taxon is held together by characters of the habit, leaves, calyx, and corolla, although there appears to be some local variation. For example, the corollas of plants from the province of Chiriquí appear to differ from the typical in being rose pink and lacking the yellow patches at the sinuses of the lower lobe; however, the characters of the leaves match those of populations elsewhere. The species is perhaps related to *Columnea gloriosa* Sprague described in 1911 from cultivated material originally collected in Costa Rica.

There are also local differences in lengths of floral parts, and leaf and calyx coloration. Variation in leaf and calyx coloration and indument may be light or age dependent. Label notes from a specimen collected by Henry Butcher, reads, ". . . new leaves light green and thin, thickening with age and changing to a pale red. . . ." The floral coloration may be actually a response to pollinator

preference, but to solve both of these problems, field studies are necessary, as the answers are not forthcoming from dried herbarium specimens.

CHIRIQUÍ: Trail from Cerro Punta to headwaters of Río Caldera, 2250–2500 m, *Allen 1428* (MO, US). Cerro Punta, 6390 ft, *Butcher* (US). Farm of Raimundo Pitti, Cerro Punta, 6300 ft, *Butcher* (US). W end of Paso de Respinga, 3 km by road SE of Bajo Grande, 4 km by air ESE of town of Cerro Punta, Chorro, 2400–2500 m, *Cochrane et al. 6315* (F, MO). Above Bajo Chorro, 1000–2000 m, *D'Arcy 11091* (MO). Alto Respinga, *D'Arcy 10101* (MO). Bajo Chorro, Boquete District, 6000 ft, *Davidson 76* (MO, US). Bajo Grande above Cerro Punta, *Dressler 4906* (PMA). Slopes of Cerro Punta, 2000 m, *Gentry 5888* (MO). Cerro Horqueta, 6500 ft, *Hagen & Hagen 2162* (NY, US). Bajo Chorro, near Río Caldera, 1900 m, *Skog & D'Arcy 4102* (MO, US). Trail to Alto Respinga above town of Cerro Punta, 2500–2800 m, *Skog et al. 4006* (US). Bajo Chorro near Río Caldera, 1900 m, *Skog et al. 4065* (US). SW slopes of Cerro Horqueta ca. 6 km NW of Boquete, 1700–1800 m, *Wilbur et al. 15441* (DUKE). Trail from Bajo Grande along Quebrada Grande to the top of Paso de Respinga on trail to Boquete, 2100–2400 m, *Wilbur et al. 15116* (DUKE, F). Ca. 1 km N of Las Nubes, E of the mountain of Cerro Punta and ca. 5 km NW of town of Cerro Punta, 2000–2300 m, *Wilbur et al. 15206* (DUKE). Upper Río Chiriquí Viejo ca. 2 km NE of Guadelupe, *Wilbur et al. 15343* (DUKE, F). E of Guadeloupe along Río Chiriquí Viejo, ca. 2 mi NE of Cerro Punta, 6500 ft, *Wilbur et al. 13084* (DUKE, MICH, MO). Above Cerro Punta toward Bajo Grande in Quebrada Bajo Grande, 6500 ft, *Wilbur et al. 10917* (DUKE). Casita Alta, Volcán de Chiriquí, 1500–2000 m, *Woodson et al. 955* (MO). Without other locality, *Butcher* (US). COCLÉ: Loma El Tigre near El Valle de Antón, *Butcher s.n.* (PMA). DARIÉN: N slopes of Cerro Pirre, 700–950 m, *Mori & Kallunki 5481* (MO). Cerro de Garagará, Sambú basin, 500–974 m, *Pittier 5625* (US). Caná-Cuasí Trail (Camp 2), Chepigana District, 2000 ft, *Terry & Terry 1540* (MO). VERAGUAS: Santa Fé slopes of Cerro Tute, 2500 ft, *Allen 4381* (MO, US). 2–7 km beyond Agriculture School Alto Piedra near Santa Fé, 500–1000 m, *Croat 25456* (MO); *Folsom 2984* (MO); *Gentry 2961* (MO); *Mori & Kallunki 2596, 2597* (both MO); *Mori et al. 3858* (MO); *Nee 11214* (MO).

27. **Columnea mira** Morley, Ann. Missouri Bot. Gard. 60: 457. 1973. TYPE: Panamá, *Dwyer et al. 7236* (MO).

Trichantha mira (Morley) Wiehl., Selbyana 1: 35. 1975.

Suffrutescent or vinelike *herbs* or *shrubs*, epiphytic; stems 3–6 mm in diam., red purple hirsute when young. *Leaves* of a pair unequal; larger leaf oblanceolate, 5.3–8.1 cm long and 2.1–2.8 cm wide, the apex acute, oblique at the base, coarsely serrate, green above but conspicuously red hirsute, 4–8 celled, also 2–3 celled white adpressed hairs, concolorous red purple beneath, densely hirsute, the hairs red, 5–9 celled, also 2–3 celled white adpressed hairs; petioles absent or to 2 mm long; smaller leaves lanceolate, acuminate, serrate, ca. 8 mm long and 3 mm wide, green above, red purple beneath. *Flowers* solitary or paired; bracts ca. 4 mm long, linear, brown reddish pilose; pedicels 1.1–1.6 cm long, brown reddish pilose; calyx lobes lanceolate, 8–10 mm long and ca. 1.5 mm wide, acuminate, 2–3 toothed, the teeth linear, to 2 mm long, green, red hirsute; corollas yellow with 2 long chocolate or red stripes running from the sinuses of the anterior lobe and two shorter pale red stripes running from the sinuses between the lateral and the posterior lobes, somewhat ventricose, ca. 4.6 cm long, 3 mm in diam. above the base, becoming ca. 1.1 cm, contracted at the throat to ca. 8 mm in diam., externally reddish pilose, the lobed portion of the corolla 9 mm long, the lobes unequal, the posterior pair connate and ca. 7 mm long, bilobed, the anterior lobe ca. 6 mm long, all lobes spreading

and linear oblong in outline; filaments yellow, glabrous, the anthers exserted, 1 mm long and 1.2 mm wide, the disc gland bilobed; ovary reddish pilose, the style reddish, glabrous, the stigma stomatomorphic. *Fruits* not seen.

Columnea mira is known only from Panamá, from the provinces of Darién and Panamá.

This species will make a most ornamental addition to the columneas now in cultivation. It differs from *C. ochroleuca* chiefly in the color of the corolla and stem vestiture.

DARIÉN: Cerro Tacarcuna, W ridge along quebrada above waterfall E of Camp, 1500–1550 m, *Gentry & Mori 14099* (MO, SCZ). Central ridge of Cerro Tacarcuna massif, 1700–1850 m, *Gentry & Mori 14131* (MO). PANAMÁ: Cerro Jefe, 3000 ft, *Butcher 1* (US); *Butcher* (PMA); *Dressler 3444* (PMA); *Duke 9387* (MO); *Dwyer et al. 4038* (DBN, MO, NY); *Dwyer et al. 7236* (MO); *Skog et al. 4215* (MO, US).

28. **Columnea moorei** Morton, Baileya 7: 55, *fig. 15*. 1959. TYPE: Cultivated, Bailey Hortorium, Cornell University, Ithaca, New York, from plants originally from Gatún, Canal Zone, *Moore* (US, holotype).

Trichantha moorei (Morton) Morton, Contr. U.S. Natl. Herb. 38: 10. 1963.
Ortholoma moorei (Morton) Wiehl., Phytologia 27: 322. 1973.

Succulent sublignose *herbs*, scandent; stems 2–4 mm in diam., minutely strigose when young. *Leaves* of a pair equal, elliptic, ca. 1.2 cm long and 7–10 mm wide, obtuse at the base and the apex, remotely crenate to entire, above green, glabrous, green or reddish beneath, strigose, the hairs transparent, 2–3 celled on the petiole, the midrib base and along leaf margins; petioles 2–3 mm long. *Flowers* solitary; bracts 1–3 mm long, linear, slightly pilose; pedicels 2.5–4.3 cm long, red, reddish pilose; calyx lobes pectinate, 1.0–1.2 cm long, 4–7 toothed, the teeth 2–3 mm long, green, red hirsute; corollas red with lateral and anterior lobes yellow or orange and 2 posterior lobes (galea) darker red, funnelform, 4.6–5.6 cm long, ca. 4 mm in diam. above the base, becoming ca. 10 mm, slightly contracted at the throat, the outside long red hirsute, the lobed portion of the corolla ca. 8 mm long, the lobes slightly unequal, the posterior pair connate, the anterior lobe reflexed, ca. 5 mm long, the lateral lobes reflexed, rounded, appendages between lobes yellow and 0.5 mm long; filaments yellow, glabrous, the anthers slightly exserted; ovary sericeous, the style yellow, slightly pilose, the stigma bilobed. *Fruits* not seen. *Chromosomes* $2n = 18$ (Fussell, 1958).

This species is known only from Panamá, from the provinces of Colón and Panamá.

COLÓN: ENE of Agua Clara rain gauge, Santa Rita lumber road, *Dressler 5296* (PMA). PANAMÁ: Cerro Jefe, 700 m, *Correa & Dressler 1171* (PMA); *D'Arcy 5242* (MO); *Dressler 3478* (PMA, PMA).

29. **Columnea nervosa** (Klotzsch ex Oerst.) Hanst., Linnaea 34: 401. 1865.

Pentadenia nervosa Klotzsch ex Oerst., Cent. Gesn. 57. 1858. TYPE: "Veragua," *Warscewicz* (not seen).

Suffrutescent *herbs*; stems shortly tomentose at the apex. *Leaves* of a pair subequal, oval elliptic, acute, obtuse at the base (?), serrulate, green, densely

tomentose above, deep violet, villous pubescent beneath; petioles short. *Flowers* longer than the villous pedicels; calyx lobes lanceolate, ca. 13 mm long, long acuminate, incised dentate, pubescent tomentose; corolla red, zygomorphic, the tube ventricose but bent, ca. 4.0 cm long, ca. 4 mm in diam. above the base, becoming ca. 11 mm in diam., contracted at the throat to ca. 7 mm in diam., pubescent, the hairs yellowish brown or red, the lobes unequal, the posterior lobes connate, erect, ca. 12 mm long, emarginate at the apex, the lateral lobes long connate with the posterior ones, broad and obtuse, the anterior lobe lanceolate oblong, porrect; disc glands 5, the posterior pair connate; anthers exserted; ovary villous.

This species is known only from the type which was probably at Berlin and no longer extant.

30. **Columnea nicaraguensis** Oerst., Cent. Gesn. 62. 1858. TYPE: San Juan, Nicaragua, *Oersted 9290* (C, holotype; MO, photo).

Suffrutescent, pendent *herbs* or *shrubs*, epiphytic; stems to 2 m or more in length, 2–7 mm in diam., more or less white sericeous. *Leaves* of a pair unequal, the larger leaf ovate, oblanceolate, lanceolate to narrowly lanceolate, 5.7–11.1 cm long and 0.6–3.5 cm wide, the apex acuminate, oblique at the base, entire, above green, sparsely strigose to almost glabrous, the hairs transparent or white, 2–3 celled, green or sometimes flushed pink or red below, sparsely sericeous, the hairs fine, transparent or reddish, 5–12 celled, more numerous especially on the veins, also 2–3 celled white adpressed hairs; petioles 1–4 mm long; smaller leaves ovate, oblanceolate, lanceolate to narrowly lanceolate, 1.0–4.7 cm long, and 4–16 mm wide, acuminate, oblique at the base, entire, vestiture as on the larger blades. *Flowers* solitary; bracts 4–9 mm long, lanceolate, creamy sericeous; pedicels 6–16 mm long, creamy sericeous; calyx lobes ovate lanceolate, 2.1–3.3 cm long, the apex long acuminate, entire or with 2–3 slight serrations near the base, green, reddish or red, sparsely sericeous, more hairy on the midrib; corollas brick red to coppery orange with yellow areas running from sinuses of the anterior lobe and at the base of the corolla, rarely concolorous red, funnelform but strongly zygomorphic, 6.1–7.7 cm long, ca. 5 mm in diam. above the base, becoming ca. 10 mm in diam. at the throat, the outside white sericeous, the lobed portion of the corolla 3.2–4.9 cm long, the lobes strongly unequal, the posterior pair connate, emarginate at the apex, 1.5–2.3 cm long, the anterior lobe 2.1–4.0 cm long, spreading; filaments minutely pilose, red, the anthers exserted; ovary sericeous, the style minutely pilose glandular, yellow, the stigma bilobed. *Fruits* white, ca. 10 mm in diameter. *Chromosomes* $2n = 18$ (Sherk, 1960).

There is considerable variation of leaf shape and size in this species; see Byrne & Morley (1976: 210).

This species is found in Nicaragua, Costa Rica, and in Panamá in the provinces of Bocas del Toro and possibly, Chiriquí.

BOCAS DEL TORO: Talamanca Valley, *Carleton 133* (US). Between Almirante and Ojo de Agua 3–6 km W of Almirante, 30–200 m, *Croat 38181* (MO). Hill above railroad station at

Milla 7.5, *Croat & Porter 16434* (MO). Changuinola Valley, *Dunlap 419, 456* (both US). Río Changuinola near Changuinola, *Dwyer 2903* (MO). Isla de Venado, Río Changuinola, *Dwyer 4383A* (GH, MO). Isla de Venado near Changuinola, *Dwyer 4625* (DBN, MO). Hillside above Almirante, *Gentry 2692* (MO, PMA). Laguna de Chiriquí, *Hart 142* (US). Quebrada Huron, 300–400 ft, *Kirkbride & Duke 438* (MO). Río Terebe between Quebrada Huron and Quebrada Schlunjik, *Kirkbride & Duke 472* (MO, REED). Río Terebe between Quebrada Treglo and Puerto Palenque, 300–350 ft, *Kirkbride & Duke 543* (MO, NY, REED, SCZ). Duwebdulup Peak N of Río Terebe, across from Quebrada Huron, 300–900 ft, *Kirkbride & Duke 572* (MO). Zigla Road at junction of Changuinola and Tuibé Rivers, *Lazor et al. 2489* (FSU, MO, SCZ). Chiriquicito to 5 mi S along Río Guarumo, *Lewis et al. 1980* (MO, SCZ). Almirante just N of Dos Milla, *McDaniel 5127* (MO). Valley of the Biarra River, Chiriquí Lagoon, *Seibert 1540* (NA). Almirante, *Sharp* (SCZ). Almirante, *Sharp & Loftin* (SCZ). Milepost 12 just E of Finca Delta (Finca 4), 12 mi W of Almirante, 20 m, *Skog & D'Arcy 4156* (E, MO, P, PMA, US). 5 km from Almirante along road from Almirante to Changuinola, 150 m, *Skog & D'Arcy 4158* (MO, US). Water Valley, *Wedel 734* (MO, US), *839* (GH, MO, US). Chiriquí Lagoon, *Wedel 1060* (GH, MO, US), *1292* (GH, MO). Fish Creek Mts., Chiriquí Lagoon, *Wedel 2252* (MO, US). Little Bocas, Chiriquí Lagoon, *Wedel 2522* (MO, US), *2557* (MO, US). Without other locality, *Carleton 256* (US). CHIRIQUÍ: Without other locality, *Hart C2 142* (K).

31. **Columnea ochroleuca** (Klotzsch ex Oerst.) Hanst., Linnaea 34: 393. 1865.

Ortholoma ochroleucum Klotzsch ex Oerst., Cent. Gesn. 51. 1858. TYPE: "Veragua," *Warscewicz* (not seen).
Trichantha ochroleuca (Klotzsch ex Oerst.) Wiehl., Selbyana 1: 35. 1975.

Suffrutescent *herbs*; stems long villous, the hairs yellowish when dried. *Leaves* of a pair unequal, the larger leaf lanceolate, 5.0–7.5 cm long and 1.4–2.0 cm wide, widest at the middle, the apex long acuminate, serrulate, adaxially hispid pilose, abaxially long villous and deep purple colored; petioles nearly lacking; smaller leaves ⅕ as long as the larger. *Flowers* shortly pedicellate, the pedicels villous; calyx lobes linear lanceolate, 9 mm long, long acuminate with a few subulate teeth, villous; corollas scarlet, ventricose, 3.6–4.0 cm long, becoming ca. 8 mm in diam., slightly contracted at the throat, pilose, the lobes slightly unequal, the posterior pair partly connate, erect, obtuse, the remainder spreading and lanceolate; anthers exserted. *Fruits* ca. 6 mm in diam., rugose ?, brown ?, globose.

This species is known only from the type which was destroyed in Berlin. The above description is adapted from the original protologue and Morton (1971a).

32. **Columnea oerstediana** Klotzsch ex Oerst., Cent. Gesn. 61, *tab.* 8, 1858. TYPE: Naranjo, Costa Rica, *Oersted 9291* (C, holotype, MO, photo; US, isotype).

Suffrutescent *herbs*, epiphytic; stems 1.5–3 mm in diam., strigose when young. *Leaves* of a pair equal, elliptic ovate, 1.2–1.6 cm long and 7–10 mm wide, the apex obtuse to acute, rounded at the base, entire, succulent, above green, glabrous, below paler green, sparsely strigose, the hairs transparent, 3–5 celled especially numerous on the veins, also 2–3 celled white or transparent hairs; petioles 1 mm long. *Flowers* solitary; bracts ca. 5 mm long; pedicels ca. 10 mm long, strigose; calyx lobes ovate, 10–15 mm long, long acuminate, 2–3 toothed, the teeth to 1 mm long, green or tinged red, strigose; corolla scarlet or red with yellow areas running from sinuses of the anterior lobe to the base of the tube, funnelform, but strongly zygomorphic, ca. 6.7 cm long, ca. 4 mm in diam. above

the base, becoming ca. 9 mm in diam. at the throat, the outside red pilose, the lobed portion of the corolla 3.1–3.6 cm long, the lobes strongly unequal, the posterior pair connate, truncate at the apex, ca. 1.8 cm long, the anterior lobe ca. 1.5 cm long, reflexed; filaments reddish or yellow, glabrous, the anthers exserted; ovary sericeous, the style yellow, pilose glandular, the stigma bilobed. *Fruits* not seen. *Chromosomes* $2n = 18$ (Fussell, 1958).

Known from Costa Rica, Panamá, French Guiana and Brazil, this species seems to be replaced mainly by *C. tenuis* in Panamá.

VERAGUAS: Santa Fé, slopes of Cerro Tute, 3000 ft, *Allen 4335* (MO, US). 0.2 mi beyond fork in road to Escuela Agricola Alto Piedra on road to Río Calovébora, 750 m, *Croat & Folsom 33893* (MO, US). 6.4 km outside of Santa Fé toward the cordillera, *Folsom 2934* (MO, US).

33. **Columnea panamensis** Morton, Ann. Missouri Bot. Gard. 26: 312. 1939. TYPE: Panamá, *Woodson et al. 860* (MO, holotype; GH, US, isotypes).

Suffrutescent *herbs* or low *shrubs*, epiphytic; stems fleshy, 5–7 mm in diam., reddish, pubescent, when older drying orange, the nodes prominent. *Leaves* of a pair subequal, elliptic, 3.2–6.0 cm long and 1.3–2.1 cm wide, the apex more or less acute, cuneate at the base, entire, green above and pilose tomentose, the hairs transparent, brown or reddish, 4–5 celled, below green, appressed pilose tomentose, the hairs transparent, brown or reddish, 3–6 cells, more numerous on the veins; petioles 5–10 mm long. *Flowers* solitary; bracts 2–3 mm long; pedicels 10–13 mm long, white to dull orange tomentose; calyx lobes lanceolate to oblanceolate, 1.2–1.7 cm long, acute, entire, green with reddish margins and tips, reddish brown pilose tomentose; corollas scarlet with orange flush along the anterior side of the tube, funnelform but strongly zygomorphic, 6.6–7.1 cm long, ca. 4 mm in diam. above the base, becoming 11 mm in diam. at the throat, externally pilose tomentose, the lobed portion of corolla 3.1–3.6 cm long, the lobes strongly unequal, the posterior pair connate, entire at the apex, ca. 1.8 cm long, the anterior lobe 1.4–1.8 cm long, spreading; filaments red or reddish, glabrous above, glandular pilose below, the anthers exserted; ovary white villous, the style pilose glandular, reddish or yellow, the stigma stomatomorphic. *Fruits* depressed globose, 1.3 cm long, 1 cm in diam., white.

This species is known only from Panamá, from the province of Chiriquí in cloud forest.

CHIRIQUÍ: Forested ridges S of Finca Lérida, 6000–7000 ft, *Allen 4763* (MO, US). Cerro Horqueta, 7000 ft, *Blum & Dwyer 2589* (MO). Above Guadeloupe NE of Cerro Punta, *Butcher* (PMA). Slopes on Cerro Horqueta, 1650 m, *Croat 26900* (MO, PMA). Above Boquete, 1650–1800 m, *Dressler & Williams 4001* (MO, PMA). Boquete, Fred Collins Finca, 6000 ft, *Ebinger 680* (MO, US); *Stern et al. 1126* (MO, US). Casita Alta, Volcán de Chiriquí 1500–2000 m, *Woodson et al. 860* (GH, MO, US). Finca Lérida, 1750 m, *Woodson & Schery 235* (MO, US).

34. **Columnea parviflora** Morton, J. Wash. Acad. Sci. 35: 127. 1945. TYPE: Tutunendo, 20 km N of Quibdó, Chocó, Colombia, *Archer 2145* (US, holotype).

Ortholoma parviflorum (Morton) Wiehl., Phytologia 27: 322. 1973.
Trichantha parviflora (Morton) Wiehl., Selbyana 1: 35. 1975.

Epiphytic *herbs* or *subshrubs*; stems erect or ascending, somewhat zig-zag, 30–35 cm long, 3–5 mm in diam., reddish, densely hirsute. *Leaves* strongly unequal in a pair, the larger leaf broadly elliptic, 4.5–9.5 cm long, 2–5 cm wide, chartaceous, the apex acute to obtuse, the base acute, oblique, serrulate, above dark green, strigose to pilose, below green or reddish; petioles 0.5–10 mm long, hirsute; smaller leaves much reduced, lanceolate, to 1 cm long. *Inflorescences* in the upper axils, of 2–5 flowers, the peduncles lacking; bracts minute; pedicels nearly sessile, less than 5 mm long, red, hirsute to sericeous. *Flowers* inconspicuous; calyx lobes distinct, unequal, orange to red, densely hirsute, the posterior lobe erect, lanceolate, 5–7 mm long, entire, the other lobes broadly ovate, 7–9 mm long, denticulate; corolla yellow, erect in the calyx, the tube gibbous at the base, cylindric above, not ventricose, 7–8 mm long, the outside sericeous, inside glabrous, the limb nearly regular, ca. 3 mm across, the lobes erect, 1 mm long; stamens included, the filaments glabrous, the anthers minute, ca. 1 mm long; disc of a single or bilobed gland; ovary pilose; style glabrous, the stigma bilobed. *Fruit* depressed globose, white, pilose, surrounded by the persistent calyx; seeds oblong, less than 1 mm long, striate, light brown.

Originally described from Colombia, *Columnea parviflora* is now believed to be more common in Panamá especially frequent in the province of Veraguas. This species has perhaps the smallest corollas of any *Columnea*, only 7–8 mm long.

COCLÉ: Summit, Alto Calvario, 7 km N of El Copé, 850 m, *Folsom & Button 3285* (US). El Petroso, at Rivera's sawmill, 7 km beyond El Copé, premontane rain forest, 800 m, *Skog et al. 4200* (US). DARIÉN: Upper gold mining camp of Tyler Kittredge on headwaters of Río Tuquesa ca. 2 air km from continental divide, *Croat 27266* (MO). PANAMÁ: Road to Cartí 19 km N of El Llano, 500 m, *Busey 899* (US). Camino de Llano a Cartí entre los 14 a 18 km de la carretera a Chepo, 400 m, *Correa et al. 1863* (PMA). VERAGUAS: Río Segundo Brazo 8 km beyond Escuela Agricola Alto Piedra beyond Santa Fé, 750 m, *Croat 25569* (MO). Beyond Río Tres Brazos 9 km from Santa Fé, *Croat 25587* (MO). Beyond Tres Brazos River along steep descent 11 km beyond Santa Fé, 650 m, *Croat 25611* (MO, PMA). Valley of Río Dos Bocas, 11 km from Escuela Agricola Alto Piedra above Santa Fé on road to Calovébora, 450 m, *Croat 27530A* (MO). First river on road between Alto Piedra School and Río Calovébora, 1.8 mi beyond school, 500 m, *Croat & Folsom 34092* (MO). Base of Cerro Tute, 6.5 km outside of Santa Fé, *Folsom 3043* (MO, US). NW of Santa Fé, 8.8 km from Escuela Agricola Alto de Piedra, on road to Calovébora, 1900 ft, *Mori 6652* (MO). 11 km from Escuela Agricola Alto de Piedra, in forest along Río Dos Bocas, Atlantic slope, *Mori & Kallunki 3127* (MO). 7 km W of Santa Fé on road past agricultural school, 2900 ft, *Nee 11154* (MO). Ca. 2 km N of Cerro Tute, *Witherspoon & Witherspoon 8828* MO, US).

35. **Columnea pectinata** Morton, Ann. Missouri Bot. Gard. 29: 50. 1942. TYPE: Panamá, *Allen 2394* (US, holotype; US, isotype).

Dalbergaria pectinata (Morton) Wiehl., Phytologia 27: 318. 1973.

Suffrutescent *herbs*, or vinelike *shrubs*, epiphytic; stems to 1 or 2 m long, 6–9 mm in diam., rugose, golden brown hirsute, the hairs red to maroon. *Leaves* of a pair strongly unequal, the larger leaf oblanceolate, 12.4–18.1 cm long and 2.9–5.3 cm wide, the apex shortly acuminate, oblique at the base, sharply serrate towards the tip, above dark green, hirsute, hairs reddish, 4–7 celled, red blotched

towards the tip and around the margin below, hirsute, the hairs reddish and more so on the veins and the leaf margins, 5–8 celled, also 2–3 celled white hairs; petioles 2–6 mm long; smaller leaves lanceolate, 0.9–2.3 cm long and 0.3–1.1. cm wide, acuminate, oblique at the base, red tipped or green below, reddish hirsute. *Flowers* several in each axil; bracts 0.6–1.4 cm long, narrow, acuminate, red to pink hirsute; pedicels 2–5 mm long, coarsely gold or brown hirsute; calyx lobes pectinate, 0.8–1.6 cm long, 4–8 toothed, the teeth 2–3 mm long, red, brown hirsute; corollas orange to scarlet, tubular, 1.6–1.9 cm long, ca. 4 mm in diam. above the base, becoming ca. 6 mm in diam., slightly contracted at the throat, the outside brown pilose, the lobes subregular, spreading to reflexed, to 2 mm long; filaments glabrous, the anthers included, yellow; ovary sericeous, the style glabrous, the stigma stomatomorphic. *Fruits* 9 mm long and 5 mm in diam. when immature, white when mature.

This species is known only from Panamá, from the province of Coclé.

COCLÉ: N rim of El Valle de Antón, 600–1000 m, *Allen 1787* (GH, MO, US). Hills N of El Valle de Antón, 1000 m, *Allen 2177* (MO, US). La Mesa N of El Valle de Antón, 1000 m, *Allen 2394* (US). N of El Valle de Antón, 1000 m, *Allen 2919* (US), *2944* (MO, US). Grass ridge known as the "Loma del Tigre," region N of El Valle, 2800 ft, *Allen 4479* (MO, US). Cerro Pilón above El Valle de Antón, *Croat 14356* (MO, NY). Hills N of El Valle de Antón, *Dressler 4382* (DUKE, MO). Cloud forest on slopes of Cerro Pilón near El Valle, 700–900 m, *Duke 12055* (MO, REED), *12107* (MO, NY, REED). 6.4 km along road to La Mesa from the El Valle main road, *Folsom & Butcher 2796* (MO). Ca. 9 km from El Valle Market beyond Sr. Furlong's finca, *Kennedy et al. 3219* (MO). La Mesa, El Valle de Antón, 1000 m, *Kennedy et al. 3010* (MO, NA, NY). Trail from La Mesa towards Las Llano and border between Coclé and Panamá, *Luteyn 4113* (DUKE). Foot of Cerro Pilón above El Valle de Antón, 2000 ft, *Porter et al. 4457A* (MO). La Mesa above El Valle, 800 m, *Skog & Butcher 4126* (E, MO, US). La Mesa 4.5 mi beyond El Valle de Antón, *Wilbur & Luteyn 11674* (DUKE, MO).

36. **Columnea pendula** (Klotzsch ex Oerst.) Hanst., Linnaea 34: 397. 1865.

Ortholoma pendulum Klotzsch ex Oerst., Cent. Gesn. 52. 1858. TYPE: "Veragua," *Warscewicz 16* (not seen).
Trichantha pendula (Klotzsch ex Oerst.) Wiehl., Selbyana 1: 35. 1975.

Suffrutescent *herbs*; stems pilose at the tip. *Leaves* of a pair subequal, the larger blade in a pair obliquely lanceolate, 7.5–10.0 cm long and 2.6–3.2 cm wide, the apex acuminate, rounded at the base, subentire, strigose pubescent above, beneath sometimes reddish, the leaves subsessile. *Flowers* ?solitary, the pedicels elongated and pendulous, recurved at the tip, longer than the flowers and ?subequal in length to the leaves; pedicels puberulent; calyx lobes linear lanceolate, ca. 16 mm long, long acuminate, subentire, pubescent; corollas red with 2 upper lobes yellow, ventricose, ca. 5.0 cm long, ca. 6 mm in diam. above the base (Morton), becoming ca. 1.5 cm in diam., contracted in the throat to ca. 11 mm in diam., almost glabrous externally, the lobes slightly unequal, the posterior pair connate, erect, rounded, the remainder subequal, spreading and rounded, ca. 1.8 cm wide; filaments longer than the corolla tube; ovary pilose.

The type was probably destroyed in Berlin. The above description was adapted from the original protologue and from Morton (1971a).

37. **Columnea perpulchra** Morton, Ann. Missouri Bot. Gard. 29: 51. 1942. TYPE: Panamá, *Allen 2305* (US).

Dalbergaria perpulchra (Morton) Wiehl., Phytologia 27: 318. 1973.

Suffrutescent *herbs* or small *shrubs*, epiphytic; stems 5–6 mm in diam., densely brown hirsute. *Leaves* of a pair strongly unequal, the larger leaf oblong to oblanceolate, 15.2–16.3 cm long and 4.4–5.4 cm wide, the apex shortly acuminate, strongly oblique at the base, serrulate, green above, pilose, the hairs transparent and reddish, 5–11 celled, red at the apex and more or less red spotted elsewhere beneath, hirsute, hairs transparent, 5–12 celled, also 2–3 celled appressed hairs; petioles 2–4 mm long, the smaller leaves ovate, 1.1–1.8 cm long and 8–10 mm wide, acuminate, strongly oblique at the base, the blades red beneath at the apex. *Flowers* solitary or paired in each axil; bracts 5–7 mm long, entire, acuminate, hirsute; pedicels 1.8–2.4 cm long, brown hirsute; calyx lobes lanceolate, 1.6–1.7 cm long, acuminate, 4–6 toothed, the teeth to 3 mm long, green, pale brown pilose; corollas yellow with red spots at the bases of the corolla lobes, funnelform, 3–4 cm long, ca. 4 mm in diam. above the base, becoming ca. 8 mm in diam., glabrous externally and internally, the lobes subregular, reflexed 5–6 mm long, sparsely strigose; filaments glabrous, the anthers included; ovary sparsely hirsute, the style glabrous, the stigma stomatomorphic. *Fruits* not seen.

This species is known only from Panamá from the provinces of Coclé, Colón, and Veraguas.

COCLÉ: Hills N of El Valle de Antón, La Mesa, 1000 m, *Allen 2305* (US). La Mesa above El Valle, 900 m, *Croat 22954* (MO, NA, NY). Cerro Pilón, *Dwyer et al. 4506* (DBN, MO). Rivera sawmill, Alto Calvario, 7 km N of El Copé, 700–900 m, *Folsom 3216* (MO, US). La Mesa above El Valle, 900 m, *Gentry 7424* (MO). Damp secondary forest at La Mesa above El Valle, 800 m, *Skog & Butcher 4120* (MO, US). El Petroso at Rivera's sawmill, 7 km beyond El Copé, 800 m, *Skog et al. 4213* (E, MO, P, PMA, US). COLÓN: Near Peluca on Río Boquerón ca. 27 km from Transisthmian Highway, *Dressler 4266* (MO, PMA, US). Near rain gauge, Santa Rita Ridge Road 14 km from Boyd-Roosevelt Highway, *Mori & Kallunki 4921* (MO, US). Dos Bocas, Río Fató valley, 40–80 m, *Pittier 4209* (US). VERAGUAS: Valley of Río Dos Bocas on road between Alto Piedra above Santa Fé and Calovébora, 350–400 m, *Croat 27361* (MO). 6.4 km outside of Santa Fé toward the cordillera, *Folsom 2992* (MO, US). Base of Cerro Tute 6.5 km outside Santa Fé, *Folsom 3030* (MO, US).

38. **Columnea polyantha** (Wiehl.) L. Skog, comb. nov.

C. silvarum Morton var. *butcheri* Morley, Ann. Missouri Bot. Gard. 60: 457. 1973. TYPE: Panamá, *Butcher* (US, holotype).

Dalbergaria polyantha Wiehl., Selbyana 2: 102. 1977. TYPE: Cultivated, Marie Selby Botanical Gardens, from plants collected in Prov. Chiriquí, Panamá, *Wiehler 7424* (SEL, holotype, not available for study).

Woody *herbs* or *shrubs*, stems to 1.5 m tall, 0.7–1.0 cm in diam., brown purplish tomentose. *Leaves* of a pair unequal, the larger leaf oblanceolate, 10.3–22.5 cm long and 2.3–4.5 cm wide, acuminate, oblique at the base, serrate, adaxially hirsute tomentose, the hairs fine and reddish, 7–10 celled, also 2–3 celled white adpressed hairs, abaxially hirsute tomentose, the hairs green or reddish, fine, 5–8 celled, lamina green above and beneath but with reddish cast from vestiture; petioles ca. 2 mm long; smaller leaves caducous, to 2.5 cm long.

Inflorescences axillary, cymose; bracts 5–10 mm long, linear, brown purple, tomentose, the pedicels to ca. 2 cm long, long brown tomentose. *Flowers* in clusters of 3–6; sepals lanceolate, ca. 8 mm long and 1 mm wide, acuminate, brown tomentose; 3–4 toothed, the teeth linear, to 1 mm long; green, corollas yellow with crescentric red marks on the lobes, funnel shaped but a little swollen, 3.7–4.3 cm long, ca. 3 mm in diam. above the base, becoming ca. 9 mm in diam., the throat contracted to ca. 5 mm in diam., the lobes slightly unequal, spreading, ca. 4 mm long, externally transparent and reddish pilose; filaments glabrous, yellow, the anthers exserted, 2 mm long and 1.5 mm wide; disc gland bilobed, the style yellow, glabrous, the stigma stomatomorphic. *Fruits* not seen.

Known from the province of Chiriquí in Panamá, and from Costa Rica, the species is very distinctive in the wild by the reddish hairs on the leaves. *Columnea polyantha* has been in cultivation since 1965.

CHIRIQUÍ: Near the village of Cuesta Piedra near Río Escarria, 3600 m, *Butcher* (US). 1 mi E of Cañas Gordas near Costa Rican border on road to Volcán, *Croat 22327* (DUKE, MO, NA, NY, USF). Barriles, 6–16 km S of Volcán, 1000–1300 m, *Dressler & Williams 3987* (PMA). Near Volcán-Río Sereno Road, 5 km from Río Sereno, *Skog et al. 4017* (MO, US), *4018* (E, MO, P, US).

39. **Columnea pulchra** (Wiehl.) L. Skog, comb. nov.

Trichantha pulchra Wiehl., Selbyana 2: 132, *pl. 36D*. 1977. TYPE: Cultivated at Marie Selby Botanical Gardens, *Wiehler 75267* (SEL, holotype, not available for study).

Epiphytic *herbs* or *subshrubs*; stems erect or ascending, to 1 m tall, commonly ca. 50 cm long, 5–10 mm in diam., more slender and often zig-zag toward the apex, the internodes green, pilose with reddish hairs. *Leaves* unequal in a pair, the larger leaf elliptic to oblanceolate, 6.5–9.8 cm long, 1.5–2.9 cm wide, fleshy, the apex rounded acute, the base cuneate, unequal, the margin nearly entire, above dark green, pilose, below pale green, suffused with pink, long hirsute; petioles 0.5–1.4 cm long, green or reddish, long pilose; smaller leaves caducous, lanceolate, to 1 cm long. *Inflorescences* in the upper leaf axils, cymose, few flowered; peduncles short or lacking; bracts small, ca. 3 mm long, lanceolate; pedicels slender, 1.0–1.5 cm long, red, hirsute. *Flowers* showy; calyx conic at the base, the lobes free nearly to the base, nearly equal, broadly elliptic to oblanceolate, 1.5–2.0 cm long, 0.5–1.0 cm wide, the apex acute, rarely or sparsely serrulate, red or orange red, hirsute; corolla light yellow, unspotted, more or less erect in the calyx, the tube nearly straight, ca. 3.5 cm long, gibbous at the base on the upper side, ca. 3 mm wide above the spur, ca. 5 mm wide at the middle, narrowing slightly at the throat, outside hirsute, inside puberulent, the limb oblique, the lobes equal, ovate, concave, 3–5 mm long, the stamens included, the filaments briefly adnate to the corolla base but connate with each other for ca. 5 mm, each ca. 3.5 cm long, yellow, glabrous, the anthers rotund; disc reduced to a bilobed dorsal gland and minute ventral glands; ovary apex pilose, the style equalling length of the stamens, glabrous, stigma stomatomorphic. *Berry* (Wiehler) globose ca. 9 mm in diam., white, pilose; seeds oblong, 1.2 mm long, striate.

Columnea pulchra appears to be most closely related to *C. calotricha* J. D. Sm.

which has a much wider range; but the species described here differs in having a corolla to nearly twice as long, or to 4 cm long, leaves rarely red beneath with prominent veins, rounded acute apically, and more nearly elliptic calyx lobes. Leaves of *C. calotricha* are usually red beneath in Panamá, with indistinct abaxial veins, apex more nearly acuminate rather than rounded acute, and oblanceolate, serrulate calyx lobes.

This species is apparently endemic to a small area in eastern Panamá on either side of the continental divide in the province of Panamá north of Chepo. *Columnea pulchra* can be found as an epiphyte in open areas at elevations of about 500 m.

PANAMÁ: Camino a Llano a Cartí, entre los 14 a 21 kms de la carretera a Chepo, 200–500 m, *Correa et al. 1861* (PMA); *Croat 22853* (US), *33739* (MO); *Dressler 4300* (MO, PMA), *4581* (PMA); *Folsom et al. 1460* (US); *Kennedy et al. 2443* (US); *Liesner 1165, 1316* (both US); *Mori et al. 4612* (MO, US); *Mori & Kallunki 5105* (MO, US); *Nee & Tyson 10951* (MO); *Skog & Folsom 4164* (US), *4177* (E, MO, P, US).

40. **Columnea purpurata** Hanst., Linnaea 34: 386. 1865. SYNTYPES: Costa Rica, *Wendland 548*; *Warszewicz 242*; *Valentini* (none seen).

C. cinnabarina Morton & Raymond, Baileya 18: 7. 1972. TYPE: Cultivated in the Montreal Botanical Garden, acc. no. 1716–65, originally collected along Río Llano Sucio, Volcán, Prov. Chiriquí, Panamá, by H. P. Butcher, *Raymond* (US, holotype; MTJB, isotype).

Suffrutescent *herbs* or *shrubs*, terrestrial and epiphytic; stems to 2 m tall, 5–10 mm in diam., yellowish hirsute. *Leaves* of a pair strongly unequal, the larger in a pair oblanceolate, 15.5–32.6 cm long and 5.4–10.7 cm wide, the apex acuminate, oblique at the base, serrate, above green, hirsute, the hairs transparent but reddish towards the leaf margins, 5–9 celled, below green, hirsute, the hairs transparent, 5–7 celled, more numerous on the veins, also 2–3 celled white appressed hairs; petioles 4–18 mm long; smaller leaves ovate, 1.2–5.0 cm long and 0.4–1.9 cm wide, long acuminate, oblique at the base, green, transparent hirsute. *Flowers* congested with many in each axil; bracts lanceolate, 1.2–3.6 cm long, subulate toothed, acuminate, orange, scarlet or greenish, reddish hirsute; pedicels 2–5 mm long, reddish hirsute; calyx lobes lanceolate, 1.7–3.2 cm long, acuminate to obtuse, 3–6 toothed, the teeth 2–5 mm long, orange to scarlet, reddish hirsute; corollas yellow or red striped, tubular, 2.4–2.7 cm long, ca. 4 mm in diam. above the base, becoming about 7 mm in diam., slightly contracted at the throat, the outside reddish to golden hirsute, the lobes subregular, erect, ca. 3 mm long; filaments glabrous below, slightly hairy above, the anthers included; ovary pilose, the style glabrous, the stigma shortly bilobed. *Fruits* ?orange, ca. 1.8 cm long and 1.0 cm in diam. *Chromosomes* $2n = 18$ (Morley, 1967).

The differences between *C. purpurata* and *C. cinnabarina* are of bract and sepal length and color and do not warrant taxonomic recognition. Some Panamanian specimens of *purpurata* have red sepals which are ca. 1.9 cm long, and there seems to be variation of intensity of pigmentation of bracts and sepals. This species is probably closely related to *C. sanguinea* (Pers.) Hanst. from northern South America and the West Indies.

Columnea purpurata is known from Costa Rica and from the provinces of

Bocas del Toro, Chiriquí, Colón, Darién, Panamá, and the Canal Zone in Panamá. In Darién the species is known as "jenerasia."

BOCAS DEL TORO: Río Teribe, between Quebrada Treglo and Puerto Palenque, 300–350 m, *Kirkbride & Duke 534* (MO, REED, SCZ). CANAL ZONE: 5 mi E of Ferry Thatcher bridge near mangrove swamp, *Lazor 3309* (FSU). Río Mendosa, ½ km upstream from Pipeline Road bridge 8 km NW of Gamboa, 100 m, *Nee 10440* (MO, US). Barro Colorado Island, *Standley 31393* (US). CHIRIQUÍ: Río Llano Sucio, Volcán, 750 ft, *Butcher* (US). COLÓN: Santa Rita Ridge Road, 3 km beyond hydrographic station, *Croat 34343* (MO). DARIÉN: Trail between Pinogana and Yavisa, 15 m, *Allen 285* (MO). La Boca de Pirre, *Bristan 1287* (MO). El Río Yape, *Bristan 1387* (MO). Gold mine at Caná, 500–600 m, *Croat 37621* (MO). Río Pirre 2.5 mi above El Real, *Duke 5073* (MO, US). 10 mi S of El Real on Río Pirre, *Duke 5456* (MO). Between Upper Río Membrillo and Camp 7 on the construction road to San Blas, 100–800 m, *Duke 10882* (MO), *10889* (MO, REED). Premontane rain forest, foothills of Cerro Cuasí, headwaters of Río Cuasí, *Duke 15643* (US). Valley between Cerro Pirre and next most southerly peak, *Folsom 4413* (MO). Río Pirre 10 mi S of El Real near Dos Bocas, *Foster & Lowenbach 2267* (F, MO, PMA, US). Trail from Pucuro to Cerro Mali, La Laguna, ridge between Pucuro and Tapalisa Rivers, 820–840 m, *Gentry & Mori 13554* (F, MO, PMA). Top of Cerro Mali, *Gentry & Mori 13650* (MO, PMA). Cerro Tacarcuna summit camp 1550–1650 m, *Gentry & Mori 14066* (MO). Manené to mouth of Río Cuasí, *Kirkbride & Bristan 1428* (MO, NY, REED). Premontane rain forest, 0–2 mi E of Tres Bocas along the shortest headwater of Río Cuasí, *Kirkbride & Duke 1151* (MO, NY, REED), *1187*, *1209* (both MO). Caná, 1750 ft, *Stern et al. 466* (GH, MO, US, US). Caná-Cuasí Trail, (Camp 1) Chepigana District, *Terry & Terry 1418* (F, MO). Pacá, *Williams 802* (NY, NY, US). PANAMÁ: Cerro Campana, 850 m, *Busey 851* (MO, NY, US); *Croat 14730* (MO); *D'Arcy & Dressler 5492* (F, MO); *Dressler 5293* (PMA); *Gentry 4920* (MO, SCZ); *Kennedy et al. 2051* (MO); *Lewis et al. 1952* (MO). Gorgas Memorial Labs yellow fever research camp ca. 25 km NE of Cerro Azul on Río Piedras, *Mori & Kallunki 3300* (MO). Cerro Campana, 825–1000 m, *Nee & Stockwell 11603* (MO); *Porter et al. 4158* (MO), *4221* (MO), *4277*, *4872* (both MO, PMA); *Skog et al. 4149* (E, MO, P, PMA, US); *Smith & Smith 3360* (US). WITHOUT LOCALITY: *Duke 6134* (MO, NY). *Hayes 955* (NY). Isthmus of Panamá, *Hayes* (GH).

41. **Columnea rubida** (Morton) Morton, Baileya 7: 58. 1959.

Alloplectus rubidus Morton, Ann. Missouri Bot. Gard. 24: 204. 1937. TYPE: Panamá, *Seibert 141* (US, holotype; MO, isotype).
Pentadenia rubida (Morton) Wiehl., Selbyana 2: 122. 1977.

Suffrutescent *herbs*, epiphytic; stems 6 mm in diam., appressed pilose. *Leaves* of a pair subequal, ovate, 10.9–14.5 cm long and 5.4–6.6 cm wide, acute, decurrent at the base, serrate denticulate, above reddish, densely pilose, the hairs reddish, 5–6 celled, also 2–3 celled white adpressed hairs, below reddish, strigose, the hairs brownish, 5–6 celled, especially numerous on the veins, also 2–3 celled white hairs especially on lamina; petioles 1.2–1.7 cm long. *Flowers* solitary; bracts ca. 3 mm long, narrow, reddish hairy, the pedicels 2.3–2.6 cm long, reddish pilose; calyx lobes lanceolate, ca. 1.6 cm long, the apex acuminate, the margins serrate, serrations 3–4, red, long pilose; corolla yellow, funnelform but a little swollen, ca. 3.2 cm long, ca. 5 mm in diam. above the base, becoming ca. 10 mm, contracted at the throat, externally pilose, the lobes subregular, rounded, erect, ca. 5 mm long; filaments slightly hairy, the anthers included; disc glands 5; ovary pilose, the style glabrous, the stigma stomatomorphic. *Fruits* not seen.

This species is known only from Panamá, from cloud forests in the province of Chiriquí.

CHIRIQUÍ: Southwestern slope of Volcán Barú, 5000 ft, *Butcher* (US). Valley of the upper Río Chiriquí Viejo, Monte Lirio, 1300–1500 m, *Seibert 141* (MO, US).

42. **Columnea rubra** Morton, Ann. Missouri Bot. Gard. 29: 52. 1942. TYPE: Panamá, *Allen 2469* (US).

Suffrutescent *herbs* or small *shrubs*, epiphytic; stems to 0.75 m tall, 5–9 mm in diam., reddish appressed pilose when young. *Leaves* of a pair unequal, the larger leaf narrowly oblong to oblanceolate, 12.6–14.5 cm long and 2.9–3.8 cm wide, the apex acute, rounded at the base, subentire, above green, glabrous, pink to claret colored beneath, strigose, the hairs brown or red, 4–7 celled, also 2–3 celled white appressed hairs; petioles 3–5 mm long, the smaller leaves ca. 1.0 cm long, soon deciduous, acuminate, green above, red beneath. *Flowers* several in each axil; bracts linear, 4–5 mm long, red, strigose; pedicels 7–11 mm long, red, strigose; calyx lobes lanceolate, 1.4–1.7(2.5) cm long, acuminate, 4–6 toothed, the teeth less than 1 mm long, green or red, the corollas yellow or with maroon to black stripes, funnelform but strongly zygomorphic, 4.5–6.0 cm long, ca. 2 mm in diam. above the base, becoming ca. 7 mm in diam. at the throat, outside pilose tomentose, the lobed portion of the corolla ca. 2.3 cm long, the lobes strongly unequal, the posterior pair connate, apiculate at the apex, ca. 1.3 cm long, the anterior lobe 1.5 cm long, reflexed, the filaments yellow, glabrous, the anthers exserted; ovary sericeous, the style glandular pilose, yellow, the stigma stomatomorphic. *Fruits* not seen.

Columnea rubra is known only from Panamá, from the provinces of Coclé, Panamá, and Veraguas. The population from Veraguas is unusual in having calyx lobes to 2.5 cm long, but in other characters the population belongs in *C. rubra*.

COCLÉ: Trail to Las Minas N of El Valle de Antón, 1000 m, *Allen 2469* (US). El Valle de Antón, 1000 m, *Allen 3411* (DBN, MO, US). Cerro Pajita, hills N of El Valle de Antón, 1000–1200 m, *Allen & Allen 4183* (MO, US). Cerro Pilón N of El Valle de Antón, *Dressler 5312* (PMA). Summit 7 km N of El Copé, Alto Calvario, 700–850 m, *Folsom 4162* (MO). PANAMÁ: Cerro Campana, *Croat 14797* (MO); *Dressler 5314* (PMA); 800–1000 m, *Gentry 4949* (MO); 800 m, *Skog et al. 4146* (MO, PMA, US). VERAGUAS: 6.4 km outside of Santa Fé on road headed toward the cordillera, *Folsom 2958* (MO, US).

43. **Columnea sanguinolenta** (Klotzsch ex Oerst.) Hanst., Linnaea 34: 389. 1865.

Stenanthus sanguinolentus Klotzsch ex Oerst., Cent. Gesn. 49. 1858. TYPE: "Veragua," Panamá, *Warscewicz* (B, not seen).
S. squarrosus Klotzsch ex Oerst., Cent. Gesn. 49. 1858. TYPE: "Veragua," Panamá, *Warscewicz* (B, not seen).
Columnea costaricensis Kuntze, Rev. Gen. 2: 471. 1891. TYPE: Puerto Limón, Costa Rica, *Kuntze* (NY).
Crantzia costaricensis (Kuntze) Fritsch, Nat. Pflanzenfam. 4(3B): 168. 1894.
Ortholoma sanguinolentum (Klotzsch ex Oerst.) Wiehl., Phytologia 27: 323. 1973.
Trichantha sanguinolenta (Klotzsch ex Oerst.) Wiehl., Selbyana 1: 35. 1975.

Suffrutescent *herbs* or *shrubs*, epiphytic or terrestrial; stems to 3 m long, 3–5 mm or more in diam., densely strigose near the tip. *Leaves* of a pair unequal, the larger leaf lanceolate to oblanceolate, 8.5–14.3 cm long and 2.5–4.4 cm wide, the apex acuminate, rounded or oblique at the base, serrulate or entire, above green, glabrous, red spotted beneath (often two spots), strigose, hairs trans-

parent, 3–9 celled, more numerous on the veins, also 2–3 celled white adpressed hairs; petioles 2–5 mm long; smaller leaves lanceolate, 0.7–2.3 cm long and 2–7 mm wide, acuminate, oblique at the base, green. *Flowers* solitary or paired; bracts lanceolate, 3–8 mm long, entire, acute, glabrous above but strigose beneath, the pedicels 1.8–4.4 cm long, transparent or reddish hirsute; calyx lobes pectinate, 2.3–3.0 cm long, 8–9 toothed. the teeth 4–8 mm long, green or reddish, reddish hirsute; corollas scarlet, ventricose, 3.8–4.4 cm long, ca. 4 mm in diam. above base, becoming ca. 1.3 cm in diam., contracted at the throat to ca. 8 mm in diam., externally sparsely reddish pilose, internally glabrous, the lobes slightly unequal, the posterior pair partly connate, the remainder spreading and 5–6 mm long; filaments papillose below, the anthers included; ovary sericeous, the style glandular above, the stigma bilobed. *Fruits* about 1.0 cm in diam.

This species is known from Costa Rica and Panamá.

BOCAS DEL TORO: Changuinola Valley, *Dunlap 449* (US). N of Río Teribe, across from Quebrada Huron behind Chief's House, 90–270 m, *Kirkbride & Duke 567A* (F, MO, SCZ). Duwebdulup Peak, N of Río Teribe across from Quebrada Huron, 300–900 ft, *Kirkbride & Duke 567B* (MO, NY, REED). Punta Róvalo to Róvalo River, *Seibert 1562* (MO, US). Water Valley, *Wedel 942* (MO, US). Chiriquí Lagoon, *Wedel 1032* (US). Water Valley, Chiriquí Lagoon, *Wedel 1513* (MO). Fish Creek Mountains, Chiriquí Lagoon, *Wedel 2310* (GH, MO, US), 2325 (MO, US).

44. **Columnea segregata** Morley, Ann. Missouri Bot. Gard. 60: 459. 1973. TYPE: Panamá, *Dressler* (US).

Suffrutescent *herbs*, epiphytic; stems 4–5 mm in diam., brown purple villous. *Leaves* of a pair unequal, the larger leaf lanceolate, 11.3–13.6 cm long and ca. 3.5 cm wide, abruptly acuminate at the apex, oblique at the base, serrulate crenulate, above green, glabrous, red spotted, blotched or concolorous red purple beneath, sericeous strigose, the hairs transparent, 4–5 celled, more numerous especially on the veins, also 2–3 celled transparent appressed; petioles 2–5 mm long; smaller leaves lanceolate, 1.2–1.8 cm long and ca. 5 mm wide, acuminate, serrate, green above and beneath. *Flowers* solitary; bracts lanceolate, 6–8 mm long, sericeous strigose; pedicels ca. 2.3 cm long; calyx lobes pectinate, ca. 2 cm long, 6–7 toothed, the teeth linear to 6 mm long, reddish, reddish pilose; corollas yellow with reddish lobes, funnelform, ca. 2.0 cm long, ca. 3 mm in diam. above the base, becoming ca. 5 mm in diam. at the throat, the outside red pilose, the lobed portion 2–3 mm long, the lobes slightly unequal, the lobes spreading, rounded; filaments not seen, the anthers included; disc gland not seen; ovary pilose, the style glandular papillose, the stigma stomatomorphic. *Fruits* ca. 7 mm in diam. (immature).

Columnea segregata is known in Panamá from the province of Chiriquí, and from Costa Rica.

Butcher (in sched.) states the corollas are about 5 cm long, but this is possibly in confusion with species in sect. *Pterygoloma.*

CHIRIQUÍ: Near Buenavista, Río Escarria, 1500 ft, *Butcher s.n.* (US). Buenavista, *Butcher s.n.* (US). Near Buenavista, S of El Hato del Volcán, *Dressler s.n.* (US).

45. **Columnea serrata** (Klotzsch ex Oerst.) Hanst., Linnaea 34: 390. 1865.

Stenanthus serratus Klotzsch ex Oerst., Cent. Gesn. 49. 1858. TYPE: "Veragua," *Warscewicz 19* (not seen).
Ortholoma serratum (Klotzsch ex Oerst.) Wiehl., Phytologia 27: 323. 1973.
Trichantha serrata (Klotzsch ex Oerst.) Wiehl., Selbyana 1: 35. 1975.

Suffrutescent *herbs*, epiphytic; stems 2–3 mm in diam., reddish hirsute villous at the apex. *Leaves* of a pair unequal, the larger leaf lanceolate to oblanceolate, 7.5–10.5 cm long and 1.5–2.5 cm wide, the apex acuminate, rounded or acuminate at the base, remotely denticulate to entire, green and glabrous above, below green and sericeous strigose, the hairs transparent 3–9 celled, more numerous on the veins; petioles 2–5 mm long; smaller leaves lanceolate, to ca. 1.0 cm long, green. *Flowers* solitary, the bracts linear, ca. 3 mm long, entire, hirsute; pedicels ca. 3 cm long, reddish hirsute; calyx lobes pectinate, ca. 2.0 cm long, 8–9 toothed, the teeth to ca. 6 mm long, reddish, reddish hirsute; corollas scarlet, ventricose, ca. 3.7 cm long, ca. 3 mm in diam. above the base, becoming ca. 10 mm in diam. in the middle and contracted to 6 mm at the throat, the outside reddish pilose, the lobes slightly unequal, the posterior pair 3 mm long, others ca. 5 mm long; filaments not seen, the anthers included; ovary pilose.

The type was destroyed in Berlin. The above description was prepared from *Pittier 16010* (BM) from Costa Rica and by adaptation from the original protologue.

46. **Columnea silvarum** Morton, Ann. Missouri Bot. Gard. 29: 53. 1942. TYPE: Panamá, *Terry & Terry 1566* (F, holotype).

Dalbergaria silvarum (Morton) Wiehl., Phytologia 27: 319. 1973.

Suffrutescent *herbs* or *shrubs*, epiphytic; stems ca. 1 m long, 4–6 mm in diam., densely red hirsute. *Leaves* of a pair unequal; larger blade oblong, 9.5–18.0 cm long and 3.7–5.6 cm wide, the apex abruptly acuminate, strongly oblique at the base, serrulate, above green, pilose, the hairs transparent and reddish, 3–6 celled, below green, hirsute, transparent but reddish near leaf margins, 5–7 celled, more numerous especially on the veins, also 2–3 celled appressed hairs; petioles 1–5 mm long; smaller leaves lanceolate, 1.0–1.4 cm long and 2–4 mm wide, acuminate at the apex, oblique at the base, green. *Flowers* in clusters of 2–5; bracts 5–9 mm long, entire, acuminate, red hirsute; pedicels 2.0–2.7 cm long, red hirsute; calyx lobes linear, 2.6–3.1 cm long, long acuminate, 2–4 toothed, the teeth 2 mm long, green or reddish, red hirsute; corollas yellow with red spots between the sinuses of the lobes, funnelform but a little swollen, 3.9–4.8 cm long, ca. 4 mm in diam. above the base, becoming ca. 10 mm in diam., externally pilose with transparent hairs, internally glabrous, the lobes subequal, spreading, 6–8 mm long; filaments glabrous, the anthers slightly exserted; style yellow, glabrous, the stigma stomatomorphic. *Fruits* 9 mm long and 6 mm in diam., green when immature.

This species is known only in Panamá from the province of Darién.

DARIÉN: Elfin forest, Cerro Campamiento S of Cerro Pirre, *Duke 15727* (US). Cerro Pirre, *Folsom 4389A* (MO, US). 0.2 mi E of Tres Bocas along shortest headwater of Río Cuasí, *Kirkbride & Duke 1163* (MO, NY, REED). Cuasí-Caná trail between Cerro Campamiento and La Escalera to "Paramo," E of Tres Bocas, *Kirkbride & Duke 1317* (MO, NY, REED). Slopes of Cerro Pirre, 700–950 m, *Mori & Kallunki 5498* (MO, US). Caná-Cuasí trail, *Terry 1499* (GH, MO). Crest Caná-Cuasí trail, Chepigana District, 5000 ft, *Terry & Terry 1566* (F).

47. **Columnea tenuis** Klotzsch ex Oerst., Cent. Gesn. 63. 1858. TYPE: "Veragua," *Warscewicz* (not seen).

C. obliqua Morton, Ann. Missouri Bot. Gard. 29: 49. 1942. TYPE: Panamá, *Woodson & Schery 607* (US, holotype; GH, MO, isotypes).

Suffrutescent *herbs* or small *shrubs*, terrestrial and epiphytic; stems 1.5–3 mm in diam., strigose when young. *Leaves* of a pair equal, ovate lanceolate, 1.5–3.3 cm long and 4–10 mm wide, the apex long acuminate, more or less oblique or rounded at the base, entire, succulent, above green, glabrous, paler green or reddish beneath, strigose, the hairs transparent, or brownish on the veins only, 4–7 celled, the veins more or less red, also 2–3 celled white adpressed hairs; petioles absent or to 2 mm long. *Flowers* solitary; bracts linear, 2–7 mm long; pedicels 6–12 mm long, reddish strigose; calyx lobes ovate lanceolate, 1.1–1.7 cm long, long acuminate, entire to 3 toothed, teeth to 1 mm long, green with red streaks or red, strigose; corolla scarlet or orange with or without yellow areas at the base of the tube or from sinuses of anterior lip, funnelform but strongly zygomorphic, 6.0–7.1 cm long, ca. 4 mm in diam. above base, becoming ca. 11 mm in diam. at the throat, the outside red pilose, the lobed portion of the corolla 3.2–3.7 cm long, the lobes strongly unequal, the posterior pair connate, truncate at the apex, 2.0–2.4 cm long, the anterior lobe 1.6–1.9 cm long, reflexed; filaments reddish, glabrous, the anthers exserted; ovary sericeous, the style reddish, pilose glandular, the stigma bilobed. *Fruit* globose, 1.0 cm in diam., 1.4 cm long, white.

This species is known only from Panamá, from the provinces of Bocas del Toro and Chiriquí.

BOCAS DEL TORO: Róbalo Trail, N slopes of Cerro Horqueta, 6000–7000 ft, *Allen 4935, 4971* (both MO, US). CHIRIQUÍ: W slopes of Cerro Horqueta, Bajo Mono-Róbalo Trail, 5000–7000 ft, *Allen 4820* (MO, US). Cerro Horqueta, 7000 ft, *Blum & Dwyer 2631* (DUKE, MO, SCZ). Cerro Otoe ca. 15–20 km N of San Félix, 3000 ft, *Bort 27* (MO). Bajo Chorro, upper Río Caldera, 6300 ft, *Butcher* (US). La Popa above Boquete, 1500–2500 m, *D'Arcy 10868* (MO, US). Bajo Chorro, Boquete District, 6000 ft, *Davidson 257* (GH, MO, US). Camp Hornitos, Fortuna dam site, 82°10'W, 8°44'N, 1000–1100 m, *Dressler 5515* (PMA). Cerro Hornitos, NE of Gualaca, 1600 m, *Dressler 5532* (PMA). San Ramón, NW of Boquete, 1700 m, *Dressler 5538* (PMA). Above Boquete, 1650–1800 m, *Dressler & Williams 4003* (PMA). NW of Boquete, Cerro Horqueta, 4500–5800 ft, *Dwyer et al. 442* (GH, MO); *Dwyer & Hayden 7717* (GH, MO); *Dwyer & Lallathin 8742* (MO). Cerro Colorado, 1500 m, *Folsom & Collins 1766* (MO, US). Cerro Horqueta, 6500 ft, *Hagen & Hagen 2132, 2163* (both NY, US). S slope of Sierra del Boquete, 4400 ft, *Maurice 855* (US). Between the Río Ladrillo and Los Siguas Camp S slope of Cerro Horqueta, 1200–1700 m, *Maxon 5407* (US). Upper Caldera River, near "Camp 1," Holcomb's trail above El Boquete, 1450–1650 m, *Maxon 5573* (US). Rocky quebrada N of San Félix, 37.2 km by road from the Panamerican Highway, *Mori & Kallunki 6004* (MO, US). Cuesta de Las Palmas, S slope of Cerro de la Horqueta, Jasmine Hill, to 200 m above Los Siguas, 1700–2100 m, *Pittier 3186* (US). NE of Boquete 5 km, 1700–1800 m, *Skog et al. 4034* (MO, US), *4044*, *4049* (both US), *4051* (MO, PMA, US), *4052*, (US), *4053* (MO, US), *4054* (E, MO, P, US). Bajo Chorro near Río Caldera, 1900 m, *Skog et al. 4059* (MO, US), *4071* (US). Bajo Chorro near Río Caldera, 1900 m, *Skog & D'Arcy*

4101 (US). Forested slopes above the village of San Ramón near Bajo Mono, 4 mi NW of Boquete, 6000 ft, *Wilbur et al. 13536* (DUKE). Above the Río Caldera beyond Bajo Mono, 1800 m, *Wilbur et al. 11062* (DUKE). Bajo Chorro, 1900 m, *Woodson & Schery 607* (GH, MO, US), *677* (MO, US).

48. **Columnea tulae** Urban, Symb. Antill. 1: 409. 1899. LECTOTYPE: Puerto Rico, *Bertero 285* (not seen).

48a. **Columnea tulae** Urban var. **tomentulosa** (Morton) Morley, Proc. Roy. Irish Acad. 74(B) 24: 438. 1974.

C. tomentosa Oerst., Cent. Gesn. 64. 1858, not *C. tomentosa* Roxb. TYPE: San Juan, Nicaragua, *Oersted 9293* (C, isotype).
C. tomentulosa Morton, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1169. 1938. Based on *Columnea tomentosa* Oerst.
C. tomentulosa Morton var. *tulae* (Urban) Morley, Ann. Missouri Bot. Gard. 60: 456. 1973, illegitimate name.

Suffrutescent *herbs*, epiphytic; stems 2–3 mm in diam., pale or dark brown tomentose. *Leaves* of a pair equal; blades elliptic to ovate elliptic, 1.5–2.8 cm long and 6–15 mm wide, fleshy, acute, decurrent at the base, entire, above green, tomentose, the hairs transparent, 3–4 celled, below green, tomentose, the hairs transparent, 4–7 celled, more pronounced on the veins, also 2–3 celled white appressed hairs, sometimes sparse; petioles 1–4 mm long. *Flowers* solitary or in 2s; bracts lanceolate, 3–5 mm long, tomentose; pedicels 8–13 mm long, red, creamy or reddish tomentose sericeous; calyx lobes ovate, 7.5–10 mm long, acuminate, more or less toothed, the teeth 4–6, to 2 mm long, green tinged with red, sericeous especially on the midribs; corolla red or orange sometimes with yellow running from the sinuses of the anterior lobe to the base of the corolla, funnelform but strongly zygomorphic, 4.0–4.7 cm long, ca. 2 mm in diam. above the base, becoming ca. 5 mm in diam. at the throat, externally reddish pilose, the lobed portion of the corolla 1.5–2.2 cm long, the lobes strongly unequal, the posterior pair connate, obtuse at the apex, 9–12 mm long, the anterior lobe 7–9 mm long, reflexed; filaments reddish, glabrous, the anthers exserted; ovary puberulous, the style yellow or reddish, pilose glandular, the stigma bilobed. *Fruits* white.

Columnea tulae var. *tomentulosa* is known from Nicaragua, Costa Rica, and Panamá; var. *tulae* occurs on Puerto Rico and Hispaniola. The Panamá collections are all from the province of Bocas del Toro.

BOCAS DEL TORO: Cricamola Valley, region of Almirante, *Cooper 206* (NY). Río Teribe between Quebrada Huron and Quebrada Schlunjik, *Kirkbride & Duke 455* (MO, MO, NY, REED, SCZ). Chiriquí Lagoon, valley of the Biarra river, *Seibert 1538* (US). Isla Colón, *Wedel 38* (GH, MO), *59*, *85* (both MO). Without other locality, *Wedel 240*, *324A*, *483* (all MO). Fish Creek Hills, Chiriquí Lagoon, *Wedel 2410* (GH, MO). Isla Colón, *Wedel 2841*, *2869* (both MO, US). Big Bight, Chiriquí Lagoon, *Wedel 2883* (MO, US). Río Cricamola, between Finca St. Louis and Konkintoë, 10–50 m, *Woodson et al. 1876* (MO, NA, NY, US).

49. **Columnea vittata** (Wiehl.) L. Skog, comb. nov.

Dalbergaria vittata Wiehl., Selbyana 2: 104, *pl. 30D*. 1977. TYPE: Cultivated, Marie Selby Botanical Gardens, from plants collected in Prov. Chiriquí, Panamá, *Wiehler 77118* (SEL, holotype, not available for study).

Epiphytic *herbs* or *subshrubs*; stems erect, ascending or spreading, to 1.3 m long, 0.9–1.3 cm in diam., green, hirsute with reddish hairs. *Leaves* unequal in a pair; larger leaf oblanceolate, 15–18 cm long, 6.0–7.5 cm wide, the apex acuminate, the base oblique, obscurely serrate dentate, above bluish green and pilose with reddish hairs, below light green, pilose; petiole 0.7–1.0 cm long, red hirsute; smaller leaf, 2.0–4.5 cm long, 0.8–2.3 cm wide. *Inflorescences* axillary reduced cymes, 4–8 flowers, the peduncle to 1 mm long; bracts lanceolate, 1.3–2.3 cm long, 0.3–0.5 cm wide, entire; pedicels 1.8–3.2 cm long, green, hirsute with reddish hairs. *Flowers* with the calyx lobes narrowly lanceolate, ca. 3 cm long, the apex acuminate subulate, sparsely long toothed, green with glandular reddish hairs; corolla yellow with red stripes, the tube spurred at the base, ca. 3.6 cm long, outside puberulous toward the base, pilose above, the inside glabrous, the lobes of the limb rounded acute, ca. 3 mm long; stamens included, the filaments 3.1 cm long, adnate to the corolla tube base for ca. 1 mm, sericeous near the base, glabrous above; disc reduced to a bilobed posterior white glabrous gland; ovary ridged longitudinally, glabrous but sericeous along the ridges, the style 3 cm long, glabrous, the stigma stomatomorphic. *Berry* oblong, acute, yellow but red spotted, sparsely sericeous; seeds oblong, ca. 1.5 mm long, striate, tawny.

The above description is adapted from the type description as no specimens attributable to the species have been seen.

50. **Columnea zebrina** Raymond, Baileya 14: 11. 1966. Based on *C. tigrina* Raymond.

C. tigrina Raymond, Mém. Jard. Bot. Montréal 57: 6. 1965, not *C. tigrina* (Karst.) Kuntze. TYPE: Cult. Montreal Botanical Garden 2762–59, from an unknown locality in Panamá, *Raymond* (MTJB, not seen).

Suffrutescent *herbs* or *shrubs*, epiphytic; stems 5–7 mm in diam., transparent appressed pilose when young. *Leaves* of a pair strongly unequal; larger blade in a pair oblanceolate, 13.5–11.8 cm long and 4.3–3.5 cm wide, the apex acute, oblique at the base, subentire, above green, glabrous, below green and suffused claret near the tip, sericeous, the hairs transparent to reddish, 5–7 celled, more numerous especially on the veins, redder near the leaf margins, also few 2–3 celled transparent appressed hairs; petioles 3 mm long; smaller leaves not seen. *Flowers* several to each axil; bracts lanceolate, 5–8 mm long, pale brown sericeous; pedicels 12–13 mm long, pale brown sericeous; calyx lobes ovate, 1.2–2.2 cm long, acute, serrulate and 1–2 toothed, the teeth to 1 mm long, greenish yellow, sometimes with reddish tips; corollas yellow or reddish with dark red stripes down the centers of the lobes and continuing to the base of the corolla tube, funnelform but strongly zygomorphic, ca. 5.8 cm long, ca. 4 mm in diam. above the base, becoming ca. 10 mm in diam. at the throat, reddish pilose outside, the lobed portion of the corolla ca. 2.5 cm long, the lobes strongly unequal, the posterior pair connate, truncate at the apex, ca. 1.1 cm long, the anterior lobe 1.5–2.0 cm long, spreading; filaments yellow, pilose, the anthers exserted, ca. 2 mm long and 1 mm wide; ovary sericeous, the style glandular

pilose, yellow, the stigma bilobed. *Fruits* white. *Chromosomes* $2n = 18$ (Lee, 1967).

This species is known only from Panamá.

COCLÉ: 2 mi N of Cerro Pilón, 900 m, *Liesner 735* (MO). COLÓN: ENE of Agua Clara rain gauge, Santa Rita lumber road, *Dressler 5295* (PMA). Río Fató, 10–100 m, *Pittier 3890* (US). DARIÉN: Cerro Campamiento S of Cerro Pirre, *Duke 15590, 15696A* (both US). Summit of Cerro Pirre, 1000–1400 m, *Gentry & Clewell 7089* (MO). Manené to mouth of Río Cuasí, *Kirkbride & Bristan 1478* (MO, NY, REED). 0–2 mi E of Tres Bocas along the shortest headwater of Río Cuasí, *Kirkbride & Duke 1166* (MO, NY, REED). PANAMÁ: Road from El Llano to Cartí-Tupile, 12–19 km above Panamerican Highway, 200–500 m, *Croat 22844* (MO, NA, NY); *Dressler 4280* (MO, PMA), *Dressler 4559* (PMA); *Mori & Kallunki 6369* (MO); *Mori et al. 4604* (MO, US), *Mori et al. 4167* (MO); *Nee 10498* (MO, US); *Nee & Dressler 9385* (MO, US); *Skog & Folsom 4172* (MO, US); *Wilbur & Luteyn 19506* (DUKE).

8. CREMOSPERMA*

Cremosperma Benth., Pl. Hartw. 234. 1846. TYPE: *C. hirsutissimum* Benth. ('hirsutissima').

Terrestrial or epiphytic perennial *herbs*; stems soft woody, short, erect, ascending or repent, pubescent. *Leaves* opposite or rarely whorled, equal to strongly unequal in a pair, lanceolate, elliptic to ovate or orbiculate, green, pubescent, the veins often prominent; petioles usually present. *Inflorescences* racemose, cymose or capitate, usually extended beyond the leaves; peduncles short or elongated; bracts lacking; pedicels usually short. *Flowers* small; calyx with a cylindric or turbinate, often 10-costate tube, the lobes 5, short, erect, entire, pubescent; corolla yellow or white to reddish, occasionally spotted, the tube more or less erect in the calyx, cylindric to funnelform, the limb 5-lobed, spreading to patent; stamens 4, included, in 2 pairs, the filaments adnate up to the middle of the corolla tube, staminode lacking; disc annular or semiannular; ovary superior. *Capsule* subglobose, membranous, dehiscing irregularly; seeds numerous, albuminous (fide Bentham).

Cremosperma occurs from Panamá south to Ecuador and includes 15 to 20 species of low growing, soft woody herbs. They are recognizable by the small congested flowers atop a usually elongate peduncle. Two species are known from Panamá. One here noted as *Cremosperma* sp. A has been annotated by Wiehler and will presumably soon be published.

The name *Cremosperma* probably refers to the albuminous seeds noted by Bentham.

Literature:

Morton, C. V. 1935. The genus *Cremosperma*. J. Wash. Acad. Sci. 25: 283–291.

———. 1938. Notes on *Cremosperma*. J. Wash. Acad. Sci. 28: 348–349.

* See *Cremosperma occidentale* Wiehl., Selbyana 5: 74, 1978.

———. 1944. Studies of tropical American plants: A revision of *Cremosperma*. Contr. U.S. Natl. Herb. 29(1): 31–35.

a. Leaves strongly unequal in a pair, the larger leaf ca. 6 × the length of the smaller, not furrowed above along the veins; inflorescences on very short peduncles not exceeding the leaves ..... 2. *C.* sp. A
aa. Leaves nearly equal in a pair, the larger leaf seldom more than 2 × the length of smaller, furrowed above along the veins; inflorescences on elongate peduncles exceeding the leaves ..... 1. *C. maculatum*

1. **Cremosperma maculatum** L. Skog, Brittonia 30: 320. 1978. TYPE: Panamá, *Mori & Kallunki 5828* (US, holotype; MO, isotype).—FIG. 14.

Herbs, either terrestrial or epiphytic in the moss layer on tree trunks; stems somewhat stoloniferous with upright branches 10(–20) cm tall, slender, 1–2 mm in diam., green villous to sericeous. *Leaves* subequal in a pair, ovate or elliptic, 1.2–2.8 cm long, 0.6–1.4 cm wide, membranous, the apex acute, the base acute to cuneate, serrate, above dark bluish green, the midveins rarely silvery, bullate, furrowed along the impressed veins, long pilose between the veins, below lighter green, appressed pilose along the prominent veins; petioles 2–9 mm long, pilose. *Inflorescences* from the upper axils but appearing terminal, exceeding the leaves, shortly cymose racemose, 4–7 flowers; peduncles slender, erect, 1.5–2.3 cm long, ca. 1 mm in diam., green, long pilose; pedicels 1–4 mm long, green, densely pilose. *Flowers* small; calyx tube obconic to turbinate, ca. 2 mm long and wide, green, pilose to sericeous, 10-costate, the lobes ovate triangular, 1 mm long and wide, green outside, pilose, inside glabrous; corollas white with purple spots or pink in the throat on the lower side, the tube funnelform, 0.7–1.2 cm long, ca. 1.5 mm in diam. at the base, ampliate above, to ca. 3 mm in diam. at the throat, outside pilose to villous, inside glandular pubescent, the limb bilabiate, the lobes obovate, the upper lobes 3 mm long, 1.5 mm wide, the lateral and the basal lobes 4 mm long, 2 mm wide, crenulate; filaments adnate to the corolla tube for ca. 8 mm above the base, curved, reddish, glabrous, the anthers broader than long, ca. 0.5 mm long, ca. 0.75 mm wide, coherent; disc annular, 1 mm high, shallowly lobed, reddish; ovary ovoid, 2 mm long, glabrous, the style 1 cm long, glabrous, the stigma stomatomorphic. Mature *fruit* and seeds not seen.

Cremosperma maculatum is known only from the province of Chiriquí in the region of Cerro Colorado at about 1,500 m. Plants grow in the thick wet humus or moss near the bases of trees or slopes and on trees where the mosses or other epiphytes produce a thick mat.

This species resembles *Cremosperma congruens* Morton from Colombia in habit and leaf form, but that species has yellow corollas and a disc reduced to a single gland.

CHIRIQUÍ: Above San Félix along mining road 18–27 mi off of Panamerican Highway, 1200–1500 m, *Croat 33071* (MO). Cerro Colorado, along mining road 31.6 km beyond bridge over Río San Félix, 1690 m, *Croat 37138* (MO). Cerro Colorado, 1500 m, *Folsom & Collins 1757* (US); *Folsom et al. 4730* (MO, US). N of San Félix at Chiriquí-Bocas del Toro border, on Cerro Colorado copper mine road along continental divide, 5000–5500 ft, *Mori & Kallunki* 5828 (MO, US).

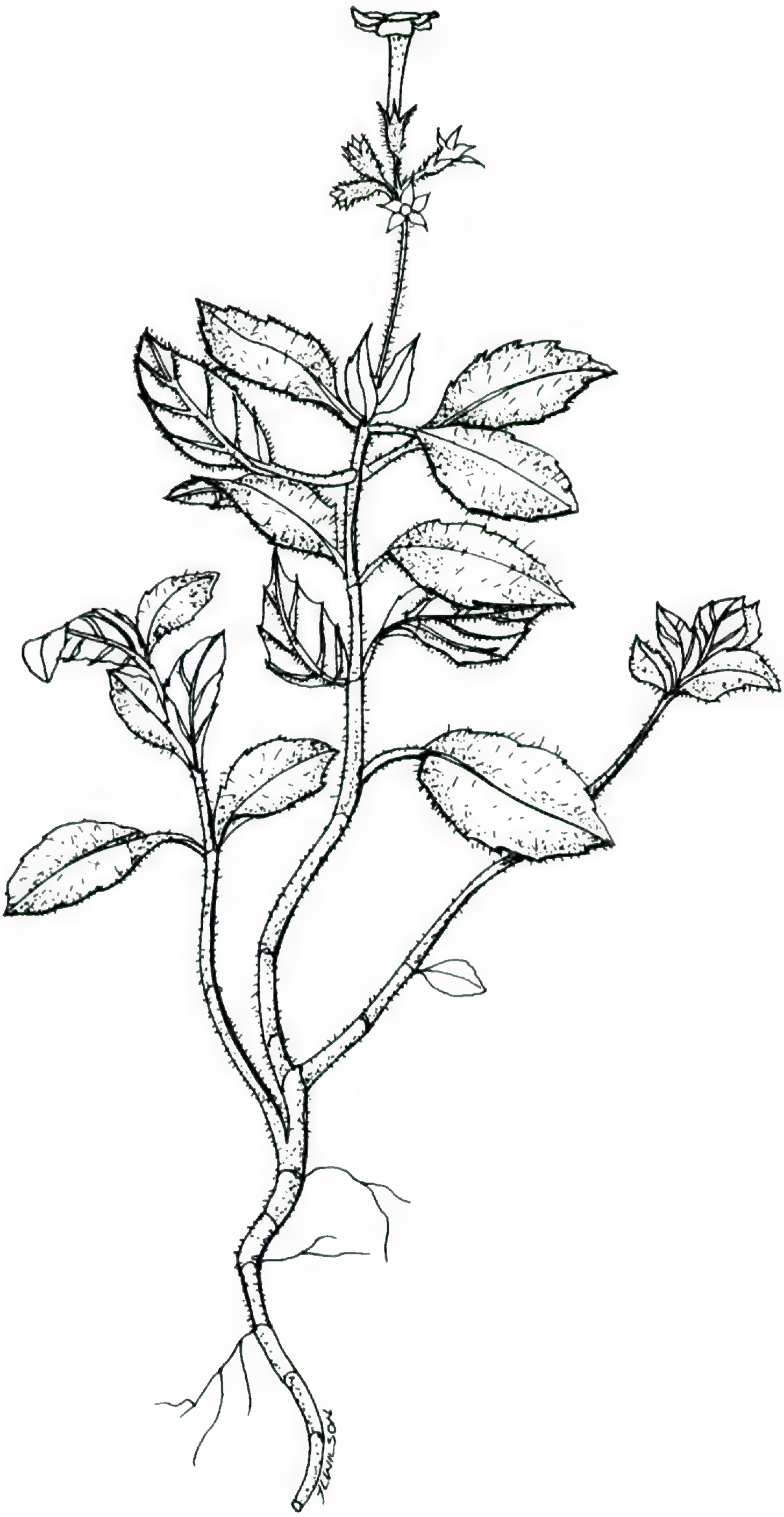

FIGURE 14. *Cremosperma maculatum* L. Skog. Habit (×1¼). [After *Mori & Kallunki* 5828 (MO).]

2. **Cremosperma** species A.*

Terrestrial or epiphytic *herbs*; stems seemingly stoloniferous and rooting at the nodes, apices and branches ascending to erect, to 10 cm tall, pilose. *Leaves* strongly unequal in a pair, the larger leaf oblanceolate to obovate, often falcate, 1.8–6.5 cm long, 0.8–2.7 cm wide, membranous, the apex acute, the base cuneate, sometimes oblique, above dark green, sparsely pilose, below lighter green, appressed pilose along the veins; petioles 3–6 mm long, villous; smaller leaves ovate, 2–7 mm long. *Inflorescences* in the upper axils, of 1–4 flowers, not exceeding the length of the leaves; peduncles and pedicels usually less than 5 mm long, rarely to 1.2 cm long, green, elongating in fruit, pilose; calyx tube narrowly obconic, 3–4 mm long, 2–3 mm wide at the top, green, velutinous, 10-costate, the lobes erect, lanceolate, 3–5 mm long, entire, green, velutinous outside, the midvein prominent, the inside glabrous; corolla white, the inside yellowish with reddish or maroon lines or stripes; tube funnelform, flattened dorsiventrally, 1.0–1.7 cm long, the base 2–3 mm in diam., ampliate from the middle to ca. 8 mm broad at the throat, the outside pilose from the middle to the limb, the inside glandular pubescent at the throat, the limb lobes obovate, 5 mm long, nearly entire; stamens included, the filaments adnate to the corolla tube for 5 mm, free part 5–6 mm long, the anthers broadly sagittate, ca. 1 mm long, 1.5 mm wide, coherent by their apices; disc annular, short, 0.5 mm long, shallowly lobate; ovary ovoid, 2 mm long, glabrous, the style to 1 cm long, glabrous, the stigma stomatomorphic. *Capsule* ovoid, ca. 4 mm long, surrounded by the persistent calyx tube; seeds fusiform to oblong, ca. 0.5 mm long, obliquely striate, dark brown.

This species differs from the other species in Panamá in having a usually much reduced peduncle with the inflorescences shorter than the leaves. Also, the leaves are strongly unequal in a pair. It is more widespread, found in the provinces of Bocas del Toro, Veraguas and Coclé. As in *Cremosperma maculatum* the plants grow in damp moss or humus in cloud forests, but at lower elevations, ca. 1000 m.

BOCAS DEL TORO: Chiriquí Trail between Gutierrez Quebrada and E slope of La Zorra, headwaters of Río Mali, *Kirkbride & Duke 725* (MO, REED). COCLÉ: Rivera's sawmill, Alto Calvario, *Folsom 3222* (MO, US). El Petroso, summit of mountain Alto Calvario, *Folsom & Collins 1543* (US). El Petroso, at Rivera's sawmill, 7 km beyond El Copé, *Skog et al. 4195* (E, MO, US), *4204* (MO, P, PMA, US). VERAGUAS: Santa Fé, forested slopes of Cerro Tute, 3000 ft, *Allen 4351* (MO). 6.4 km outside of Santa Fé, *Folsom 2967* (MO, US). Ridgetop Cerro Tute, ca. 10 km NW of Santa Fé, 1000 m, *Mori 6748* (MO). Road from Santa Fé to Calovébora, 16 km from Santa Fé, *Mori et al. 6702* (MO). Ridge top below summit of Cerro Tute, NW of Santa Fé, *Mori & Kallunki 5268* (MO). 7 km W of Santa Fé on road past Agricultural school, 2900 ft, *Nee 11258* (MO).

9. DIASTEMA

Diastema Benth., Bot. Voy. Sulphur 132. 1845. TYPE: *D. racemiferum* Benth.

Diastemella Oerst., Cent. Gesn. 25. 1858. TYPE: *D. bracteosa* Oerst. = *Diastema hispidum* (DC.) Fritsch.

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* See *Cremosperma* species A = *C. veraguanum* Wiehl., Selbyana 5: 76 ('veraquense'). 1978.

Slender perennial *herbs* from scaly rhizomes; stems short, unbranched, hirsute or villous. *Leaves* opposite, nearly equal in a pair, membranous, coarsely crenate, dentate, or serrate; petioles usually elongate. *Inflorescences* axillary or terminal racemes, pedunculate, bracteate. *Flowers* few; floral tube turbinate; calyx 5-lobed, each lobe free, elongate, often spreading, entire, green; corolla white, sometimes with purple markings, tubular, funnelform or cylindric, erect in the calyx, neither spurred nor ventricose, only slightly broader toward the limb, the limb of 5 rounded lobes, terminal, regular or slightly bilabiate; stamens 4, with a small staminode, the filaments adnate to the base of the corolla tube, the anthers orbicular, at first coherent by their apices, later discrete, thecae slender, dehiscent by slits above; disc of 5 glands sometimes connate into 2–3 glands; ovary ½-inferior; style elongate, slender, the stigma bilobed. *Fruit* an obovoid capsule, membranous, the apex convex, 2-valved; seeds numerous, minute.

About 40 species of *Diastema* have been reported but this number would likely be reduced in a careful study of the genus. Five or six are known in cultivation. *Diastema* ranges from México to northern South America.

Bentham probably adopted the generic name from the Greek word *diastema* either to refer to the separated anthers, or else he believed that the genus fills the interval or space between *Achimenes* and *Kohleria*.

Literature:

Batcheller, F. N. 1969. Gesneriads one by one: *Diastema*. The Gloxinian 19(2): 11–14.

a. Peduncles usually exceeding pedicels; inflorescences usually terminal, exceeding the leaves; dried leaves translucent ..... 2. *D. racemiferum*
aa. Peduncles always shorter than pedicels; inflorescences usually axillary or terminating lateral branches, shorter than the leaves; dried leaves opaque.
  b. Leaves nearly glabrous, thickened; floral tube narrowly funnelform .... 3. *D. scabrum*
  bb. Leaves pilose to hispid, membranous; floral tube and fruit globose .... 1. *D. hispidum*

1. **Diastema hispidum** (DC.) Fritsch,[11] Bot. Jahrb. Syst. 50: 407. 1913.

Episcia hispida DC., Prodr. 7: 547. 1839. TYPE: "Brasil?" [probably from Peru and a duplicate of *Poeppig 1031*], *Poeppig* (G-DC, holotype not seen; BH, fragment; US, photo).
Diastemella bracteosa Oerst., Cent. Gesn. 26. 1858. TYPE: Aguacate, Costa Rica, *Oersted 9315* (C, holotype; IDC 2204–2. 72: II 6).
Diastema bracteosum (Oerst.) Hanst., Linnaea 34: 438. 1865.
D. micranthum J. D. Smith, Bot. Gaz. (Crawfordsville) 61: 377. 1916. TYPE: Collinas de Jérico, Santa Clara, Costa Rica, *Pittier 7602* (CR, holotype; US, isotype).

Slender *herbs*; stem erect to repent or decumbent, rooting at the nodes, to 15 cm tall; internodes to 5 cm long, reddish toward the lower part, green upwardly, densely pilose. *Leaves* ovate, 2.5–6.6 cm long, 1.4–3.8 cm wide, the apex acute, the base occasionally oblique, acute to truncate, crenate to serrate, medium green above, pilose to hispid, beneath lighter green, pilose, densely pilose along the veins; petioles 0.5–1.8 cm long, green or reddish, pilose. *Inflorescences* commonly in each axil, cymose or racemose, of 1–4 flowers, the peduncles short or

[11] Only those names attributed to Central American plants are included.

lacking, flowers then appearing fasciculate; bracts lanceolate, 2–5 mm long, green, pilose; pedicels 0.8–1.5 cm long, elongating in fruit, green, pilose. *Flowers* with a globose floral tube, ca. 4 mm in diam., pilose; calyx lobes lanceolate, 2–5 mm long, 0.5–1.5 mm wide, the corolla white with purple spots within or with lines or spots on the limb, the tube funnelform to cylindric, 0.9–1.8 cm long, pilose, the lobes ca. 1.5 mm long; stamens with the anther locules orbicular; disc of 5 broadly linear glands shorter than the apex of the ovary; style equalling the length of the corolla tube. *Capsule* globose; seeds dark reddish brown, rhombic.

In Panamá, *Diastema hispidum* is rare, known only from the province of Veraguas, also the provenance of *D. scabrum*. As with *D. scabrum*, this species is found also in Peru as well as north through Colombia and Central America to Costa Rica. Its habitat is on damp rocks near streams.

VERAGUAS: Guabal, Río Dos Bocas, 16 km NW of Santa Fé, 500 m, *Dressler 5017* (PMA). Base of Cerro Tuti, *Folsom 3016* (MO, US). Road to Calovébora NW of Santa Fé 2.7 km from Escuela Agricola Alto de Piedra, *Mori & Kallunki 5339* (MO).

2. **Diastema racemiferum** Benth.,[12] Bot. Voy. Sulphur 132. 1845 ('*racemifera*'). TYPE: Island of Salango, Ecuador (not seen).—FIG. 15.

D. cristatum Hanst., Linnaea 34: 438. 1865. SYNTYPES: *Hoffman 692*; *Friedrichsthal 168* [*1271*] (not seen).
D. eggersianum Fritsch, Bot. Jahrb. Syst. 50: 405. 1913. TYPE: Near Hacienda El Recreo, Prov. Manabi, Ecuador, *Eggers 15021* (US, isotype).
D. rupestre T. S. Brandeg., Univ. Calif. Publ. Bot. 6: 65. 1914. TYPE: Finca Mexiquito, Chiapas, México, *Purpus 6849* (US, isotype).
D. exiguum Morton, Ann. Missouri Bot. Gard. 24: 202. 1937. TYPE: Panamá, *Seibert 579* (US, holotype; MO, isotype).
D. exiguum var. *lilacinum* Morton, Ann. Missouri Bot. Gard. 24: 202. 1937. TYPE: Panamá, *Seibert 432* (US, holotype; MO, isotype).

Small *herbs*; stems erect, 2–25 cm tall, glabrous to sparsely covered with white hairs, the internodes often reddish. *Leaves* sometimes appearing crowded at the apex of the stem; blades lanceolate to ovate, elliptic, or oblong, membranous, translucent when dry, 1.5–13.5 cm long, 0.9–6.4 cm wide, the apex obtuse or acute, the base sometimes oblique, rounded to acute, the margin various, crenate, dentate, serrate to biserrate, above medium green, sparsely pilose to glabrescent, beneath lighter green to whitish, sparsely pubescent at least on the veins, to glabrous; petioles 0.5–6.5 cm long, green or reddish, glabrate. *Inflorescences* numerous, one to an axil and terminal or only terminal, erect, racemose, 3–15 cm long; peduncles usually elongate but often equalling the petiole of the subtending leaf, green or reddish, glabrate bracts and bracteoles clasping the pedicels, lanceolate or ovate, ca. 5 mm long and 2 mm wide; pedicels slender, usually shorter than the peduncles. *Flowers* several per inflorescence; floral tube shallowly funnelform at anthesis, ca. 1 mm long, ca. 2 mm wide, elongating in fruit, green, glabrescent; calyx lobes linear lanceolate, 2–4 mm long, rarely more, ca. 1 mm wide, acute, glabrate or sparsely strigose; corolla tube slender, 1.0–1.8 cm long, ca. 3 mm wide just above the base, broadening to ca. 6 mm wide below the

[12] Only names attributed to Central American plants have been included.

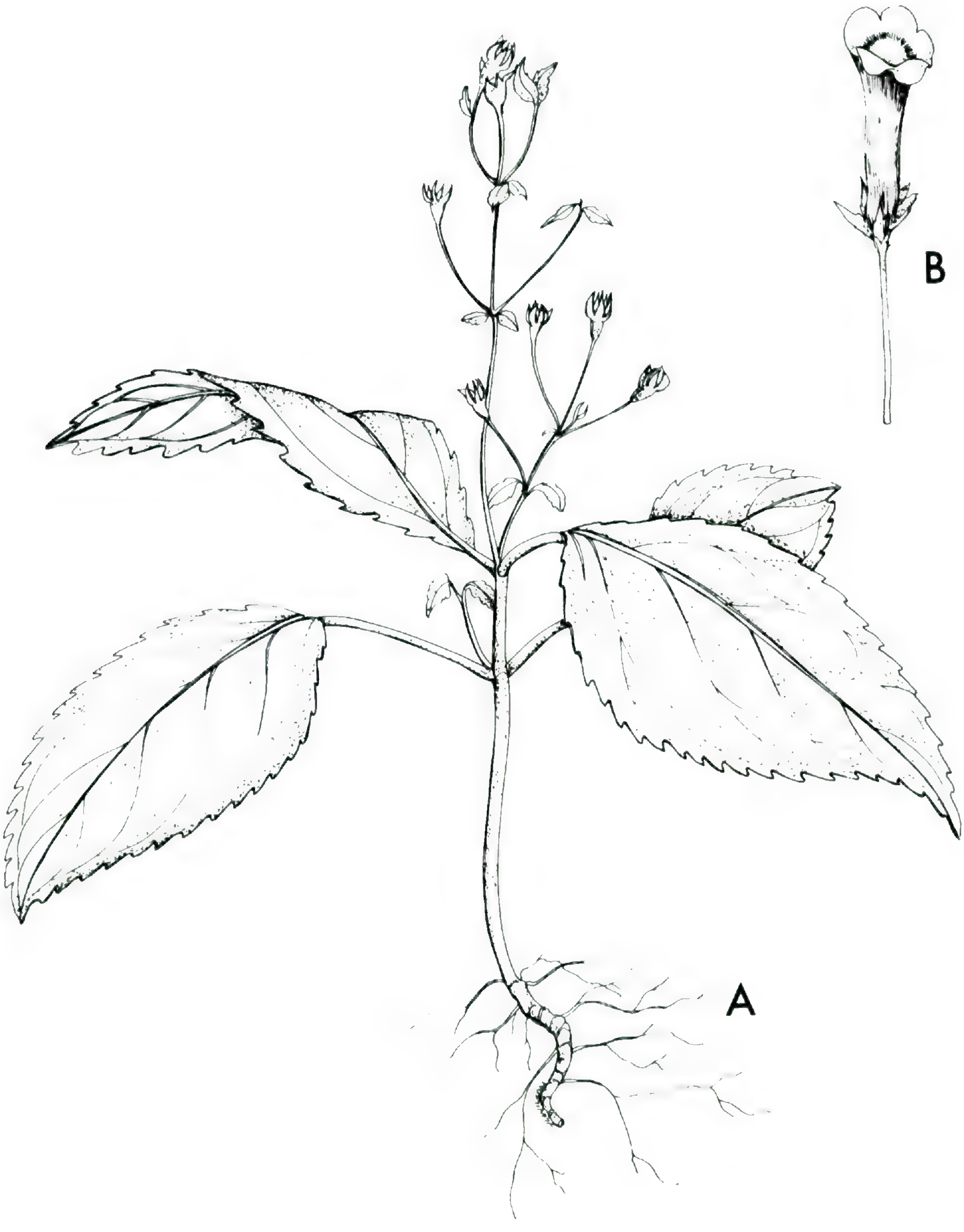

FIGURE 15. *Diastema racemiferum* Benth.—A. Habit (×7/10).—B. Flower (×1⅜). [After *Witherspoon & Witherspoon 8749* (US).]

limb, white or yellow, especially near the base outside, inside yellowish, occasionally with a few purple spots near the limb, or lavender or pinkish with a white limb, nearly glabrous to sparsely pilose near the limb, the lobes rounded, 2–3 mm long; stamens 4, didynamous, included; disc glands 5, often equalling the ovary, linear clavate; ovary apex sparsely pilose to glabrescent, the style equalling the

length of the stamens, glabrous or puberulent. *Capsule* obovoid, 2-valved; seeds rhomboid to fusiform, dark reddish brown, striate.

Diastema racemiferum Benth. ranges from México to Panamá, Venezuela and Ecuador, on limestone rocks in damp places at low elevations or in secondary wet forests.

Although I have not seen the type specimen at BM—a collection presumably by Hinds from the Island of Salango, Ecuador, and described by Bentham—US has a duplicate of a collection by Barclay (*644*) from the same locality. Since Barclay was the botanist on the voyage of the H.M.S. Sulphur, it is likely that *Barclay 644* was collected from the same population as the type. The plants from Panamá are not easily distinguishable from those from Ecuador and agree with the species description of *D. racemiferum.* Numerous synonyms can be included in this species. Most of the synonyms represent variation in floral coloration and vegetative vestiture. These cannot be separated geographically. Indeed, extreme variants may be found in the same colony. This variation is not uncommon in other genera, e.g., *Gloxinia* and *Monopyle.*

CANAL ZONE: On limestone rocks, Mohinga Swamp, lower Chagres River, *Bartlett & Lasser 16863* (MICH, MO). Drowned forest of Quebrada Bonita, 70–80 m, *Dodge & Allen 17073* (MO). Salamanca Hydrographic Station on the gorge of the Río Pequení, 70–80 m, *Dodge et al. 16965* (MO). Madden Dam, *Ebinger 859* (F, MO, US). Barro Colorado Island, *Kenoyer 539a* (US). Río Petitpie from road to Ft. Sherman from Gatún Locks (S2 or 82), *Mori & Kallunki 2669* (MO). Las Cruces, 26–40 m, *Seibert 579* (MO, US). Hills W of the Canal near Gatún, *Standley 27223* (US). Madden Lake, *Witherspoon & Witherspoon 8794* (MO). Salamanca Hydrographic Station, Río Pequení, 80 m, *Woodson et al. 1575* (MO, US). CHIRIQUÍ: Cerro Colorado, 50 km N of San Félix, near mining camp, 650–800 m, *Dressler* (PMA). Ridge road at Cerro Colorado 4.3 km from main road, 1450–1750 m, *Folsom et al. 4805* (MO, US). COCLÉ: El Valle, 800–1000 m, *Allen 737* (MO). Hills N of El Valle de Antón, *Dressler 4095* (MO, US). El Valle de Antón, 500–700 m, *Seibert 432* (MO, US). Quebrada Amarillo N of El Valle, *Witherspoon & Witherspoon 8749* (MO, US). DARIÉN: Río Chico, from Yavisa to ca. one hour by outboard, *Burch et al. 1089* (MO). Cerro Pirre, *Folsom 4408* (MO, US). Above Pacá, *Williams 709* (NY, US). PANAMÁ: Alhajuela, *Cornman 2008* (US). Between Río Bayano dam & Cañita, *D'Arcy 9393* (MO). 3 km E of Cañita toward Bayano dam site, *Dressler 4136* (MO, US). Panamerican Highway, near Jeniné, Río Cañita, *Duke 3861* (MO). Río Chagres 1 mi above Madden Lake, *Duke 4471* (MO, US). Gallery along Río Teralbe, near Panamerican Highway and El Llano, *Duke 5666* (MO, PMA). Between Cañasas and Sábalo, 100 m, *Duke 14464* (MO). Shaded rocks along Río Merino, San José Island, *Erlanson 542* (NA, US). Deep forested ravine N of Red Hill, San José Island, *Johnston 128* (US).

3. **Diastema scabrum** (Poepp.) Benth. ex Walp., Repert. Bot. Syst. 6: 401, 403. 1847.

Trevirana scabra Poepp. in Poepp. & Endl., Nov. Gen. 3: 8. 1840. TYPE: Peru, *Poeppig 1583* (W, holotype; US, photo).

Achimenes scabra (Poepp.) Walp., Repert. Bot. Syst. 2: 719. 1843.

Erect or decumbent succulent *herbs*; stems to 15 cm tall, 2–3 mm in diam., the internodes 2–4 cm long, green or occasionally reddish, puberulent; branches occasional. *Leaves* somewhat thickened, lanceolate to elliptic, 3.0–7.5 cm long, 1.6–4.2 cm wide, the apex acute, the base oblique, acute, dentate to serrate, the upper surface dark green, sparsely strigose, the hairs appearing to be in rows between the major lateral veins, the lower surface light green, puberulent with transparent hairs; petioles ca. 1 cm long, green, puberulent. *Inflorescences* terminat-

ing the branches or rarely the main axis, racemose, the peduncles short, usually much less than 1 cm long, green or reddish, puberulent; bracts leaflike and often clasping the pedicels, ca. 5 mm long, 1–2 mm wide, green, the pedicels ca. 3 times as long as the peduncle or more, slender but expanding gradually toward the floral tube, 1–2 cm long. *Flowers* several per inflorescence; floral tube narrowly funnelform, elongated below the calyx lobes, to 5 mm long, 2 mm wide below the lobes, green, the veins prominent, puberulent; calyx lobes oblong, 5–7 mm long, ca. 2 mm wide, obtuse, green, sparsely strigose outside, the inside glabrous; corolla tube yellow with a cream colored limb, the tube 1.0–1.5 cm long, glabrous below, sparsely strigose above outside; ovary reddish, pilose toward the apex, style sparsely pilose. *Capsule* ovoid; seeds ellipsoid, dark reddish brown, striate.

Diastema scabrum is so far known only from Peru and in Panamá from Coclé and Veraguas provinces. It may be expected elsewhere in Panamá and northwestern South America. As in the other Panamanian species of *Diastema*, plants are found in moist rocky areas on hillsides or near streams.

COCLÉ: Hills N of El Valle de Antón, *Dressler 4096* (US). VERAGUAS: Guabal between Continental Divide and Río Calovébora, NW of Santa Fé, 400–500 m, *Dressler 4720* (PMA).

10. DRYMONIA*

Drymonia Mart., Nov. Gen. 3: 57. 1829. TYPE: *D. calcarata* Mart.

Macrochlamys Decne., Rev. Hort. 21 [sér. 3, 3]: 243. 1849. TYPE: *M. patrisii* (DC.) Decne. = *Drymonia coccinea* (Aubl.) Wiehl.

Erythranthus Oerst. ex Hanst., Linnaea 26: 183, 208–209. 1854. TYPE: *E. coriaceus* Oerst. ex Hanst. = *Drymonia coriacea* (Oerst. ex Hanst.) Wiehl.

Calanthus Oerst. ex Hanst., Linnaea 26: 184, 208–209. 1854. TYPE: *Calanthus multiflorus* Oerst. ex Hanst. = *Drymonia multiflora* (Oerst. ex Hanst.) Wiehl.

Polythysania Hanst., Linnaea 26: 184, 208–209. 1854. TYPE: *P. parviflora* Hanst. = *Drymonia hansteiniana* Wiehl.

Saccoplectus Oerst., Cent. Gesn. 43. 1858. TYPE: *S. strigosus* Oerst. = *Drymonia strigosa* (Oerst.) Wiehl.

Caloplectus Oerst., Cent. Gesn. 45. 1858. TYPE: *C. macrophyllus* Oerst. = *Drymonia macrophylla* (Oerst.) H. E. Moore.

Anisoplectus Oerst., Cent. Gesn. 46. 1858. TYPE: *Alloplectus pendulus* Poepp. = *Drymonia pendula* (Poepp.) Wiehl.

Alloplectus Mart. subgen. *Calanthus* (Oerst. ex Hanst.) Hanst., Linnaea 34: 361. 1865.

Alloplectus Mart. subgen. *Erythranthus* (Oerst. ex Hanst.) Hanst., Linnaea 34: 362. 1865.

Crantzia Scop. sect. *Calanthus* (Oerst. ex Hanst.) Fritsch in Engler & Prantl, Nat. Pflanzenfam. 4(3b): 168. 1894.

Crantzia Scop. sect. *Macrochlamys* (Decne.) Fritsch in Engler & Prantl, Nat. Pflanzenfam. 4(3b): 168. 1894.

Alloplectus Mart. sect. *Macrochlamys* (Decne.) Dalla Torre & Harms, Gen. Siphon. 474. 1904.

Terrestrial or epiphytic *shrubs* or *lianas*; stems quadrangular or terete, up to 5 m long when climbing, often with spreading adventitious roots in the internodes; branches present or lacking. *Leaves* opposite, equal or nearly equal in a pair, membranous or rarely coriaceous; petioles sometimes elongate. *Inflorescences* axillary, of single flowers or several in a cluster; bracts often large and leaflike, or small and inconspicuous, but often caducous. *Flowers* often

* See *Drymonia dressleri* Wiehl., Selbyana 5: 80. 1978, and *D. microphylla* Wiehl., Selbyana 5: 81. 1978.

showy and brightly colored; sepals 5, often large and colored or leaflike, free or briefly connate at the base, unequal with the uppermost shortest; corolla oblique in the calyx, usually funnelform and broader toward the mouth, spurred or saccate at the base, the throat broad, the limb of 5 lobes, usually spreading, rounded, often fimbriate, the 3 basal lobes usually exceeding the 2 upper lobes; stamens 4, adnate to the base of the corolla tube, didynamous, included, the filaments occasionally contorted, the anthers sagittate, broadest at the tip, narrowed toward the base to 2 separate spurs, before anthesis coherent by sides and faces with the spurred bases up, dehiscing by 2 to 4 pores, after anthesis the filaments coiling and the anthers separating; disc reduced to a single posterior gland; ovary superior, the style included, the stigma stomatomorphic or 2-lobed. *Fruit* a fleshy capsule, becoming coriaceous, dehiscing by 2 valves that recoil to reveal a red, orange, or purple interior and a mass of seeds in a pulpy funicle; seeds ellipsoid or fusiform, obliquely striate.

The genus *Drymonia* is one of the largest gesneriad genera in the neotropics with nearly a hundred species. Plants of *Drymonia* are usually lianas, which distinguishes the genus from most other Gesneriaceae. Another distinguishing character is the specialized porate dehiscence of the stamens described by Moore (1955). Species may be found throughout the continental neotropics and the Lesser Antilles, in moist forests from a probable center of distribution in Colombia and Ecuador.

Drymonia was named by Martius based on the Greek word *Drymos* = forest, referring to a plant of the forest.

Literature:

Moore, H. E. 1955. *Drymonia macrophylla*. Baileya 3: 109–112.

a. Calyx lobes entire or at most serrulate; leaves sometimes coriaceous.
  b. Leaves glabrous above.
    c. Calyx green or white.
      d. Corolla dark red or maroon, with a white or yellow area inside; calyx lobes broadly ovate, usually more than 1 cm wide and 2 cm long; pedicels shorter than the calyx ..... 12. *D. rubra*
      dd. Corolla yellow, white or pale green, sometimes reddish inside; calyx lobes lanceolate or ovate, usually less than 1 cm wide and 2 cm long; pedicels shorter or longer than the calyx.
        e. Corolla streaked with reddish or orange longitudinal lines on or within tube ..... 1. *D. aciculata*
        ee. Corolla unstreaked or with a reddish patch.
          f. Pedicels longer than the calyx lobes, lobes ovate, without a prominent midvein; corolla yellow; leaves broadly elliptic ..... 15. *D. sulphurea*
          ff. Pedicels shorter than the calyx lobes, lobes narrowly lanceolate to lanceolate, with or without a prominent midvein; corolla white to cream; leaves lanceolate or narrowly elliptic with darker veins.
            g. Leaves subcoriaceous; midvein of calyx lobes not prominent ..... 14. *D. stenophylla*
            gg. Leaves membranous; midvein of calyx lobes prominent ..... 18. *D. warscewicziana*
    cc. Calyx red, pink, or purplish.
      h. Corolla tomentose outside, strongly ventricose with a small throat;

inflorescences congested in leaf axils on short pedicels; bracts numerous, leaves coriaceous ..... 4. *D. coriacea*

hh. Corolla nearly glabrous, at most puberulent, not strongly ventricose; inflorescences of few flowers not congested in the leaf axils, or on long pedicels; bracts few or lacking; leaves coriaceous or not.

i. Corolla yellow or cream.

j. Leaves purplish beneath ..... 16. *D. turrialvae*

jj. Leaves green beneath ..... 1. *D. aciculata*

ii. Corolla purplish or red ..... 3. *D. conchocalyx*

bb. Leaves pubescent above.

k. Plants terrestrial, herbs or subshrubs; corolla white to yellow; leaves membranous ..... 7. *D. lanceolata*

kk. Plants epiphytic or climbing, shrubs or lianas; corolla red, white with reddish lobes, white with yellow throat, or all white (but then leaves entire), or yellow; leaves succulent to coriaceous.

l. Leaves entire.

m. Calyx lobes more than 2 cm long; corolla red or yellow.

n. Corolla dark red ..... 12. *D. rubra*

nn. Corolla yellow ..... 5. *D. flavida*

mm. Calyx lobes ca. 1 cm long; corolla white, rarely with reddish lobes ..... 14. *D. stenophylla*

ll. Leaf margins serrulate to serrate.

o. Stem or branch apices brown hirsute; corolla hirsute outside, ca. twice as long as the calyx ..... 2. *D. alloplectoides*

oo. Stem or branch apices at most puberulous or minutely strigillose; corolla puberulent outside, either scarcely exceeding the calyx to more than twice as long.

p. Corolla scarcely exceeding calyx; calyx lobes serrulate or denticulate, or sinuate, apex acuminate or acute; leaves seldom more than 15 cm long ..... 13. *D. serrulata*

pp. Corolla greatly exceeding calyx; calyx lobes entire, apex obtuse; leaves usually more than 15 cm long ..... 8. *D. macrantha*

aa. Calyx lobes variously toothed, serrate or pectinate; leaves never coriaceous.

q. Inflorescences of single flowers.

r. Leaf blades glabrous and light green below, not bullate above.

s. Corolla 3.0–3.6 cm long; calyx lobes serrate; leaves ovate or elliptic ..... 6. *D. folsomii*

ss. Corolla ca. 2.5 cm long; calyx lobes deeply toothed; leaves mostly lanceolate ..... 10. *D. multiflora*

rr. Leaf blades villous or appressed pilose and mostly reddish to purple below, bullate or not above.

t. Calyx lobes broadly ovate, cordate at base; leaves not bullate above ..... 19. *D.* sp. A

tt. Calyx lobes oblong, not cordate at base; leaves bullate above ..... 17. *D. variegata*

qq. Inflorescences of more than one flower.

u. Calyx lobes deeply and conspicuously toothed; corolla white or pale yellow ..... 9. *D. macrophylla*

uu. Calyx lobes shallowly toothed; corolla yellow at least in the throat ..... 11. *D. parviflora*

1. **Drymonia aciculata** Wiehl., Selbyana 2: 105. 1977. TYPE: Cerro Jefe, Prov. Panamá, Panamá, *Wiehler & Dressler 71189* (SEL, holotype, not available for study).

Epiphytic *shrubs* or *lianas*; stem erect, to 5 m long, the internodes 1.5–7.0 cm long, green or reddish brown, glabrous. *Leaves* nearly equal to greatly unequal in a pair, narrowly or broadly elliptic, ovate, obovate or lanceolate, 7–18 cm long, 2.3–10.0 cm wide, subcoriaceous, the apex acute to abruptly acuminate, the base

acute to rounded, entire, above dark green, glabrous, below lighter green with minute dots and prominent veins; petiole 1–4 cm long, glabrous. *Inflorescences* axillary of one or few flowers; peduncle not obvious; bracts linear, ca. 0.5 cm long; pedicels ca. 1 cm long, reddish, minutely strigillose. *Flowers* with the calyx oblique, the lobes unequal, lanceolate, ca. 2 cm long, 0.5–1 cm wide, reddish or rarely green, strigillose at the base, glabrous toward the acuminate apex; corolla white or cream colored with reddish or orange lines on the limb and within the tube, the tube oblique in the calyx, 3.0–4.5 cm long, the base saccate, broader toward the limb, glabrous, the lobes of the limb suborbiculate, ca. 1 cm long, erose, the basal lobe almost fimbriate, glandular; stamens included, the filaments 2–3 cm long, glabrous, the anthers oblong; disc gland white, glabrous; ovary ovoid, finely white sericeous, the hairs appearing to be in rows on dried material, the style glabrous, the stigma stomatomorphic. *Capsule* not seen.

Drymonia aciculata is known from the province of Panamá at an elevation of usually less than 500 m in wet forests. The species has been reported from Veraguas but no specimens have been seen from there.

One of the paratypes cited by Wiehler for this species, *Kirkbride & Duke 794*, from Bocas del Toro is *Drymonia conchocalyx* Hanst.

PANAMÁ: El Llano-Cartí road 7–12 km from Panamerican Highway, 360–400 m, *Croat 25097* (MO). La Eneida, region of Cerro Jefe, *Dressler 3293* (PMA). Cerro Jefe, 800–1000 m, *Folsom & Hartman 4629* (MO, US); *Mori & Kallunki 2771* (MO). El Llano-Cartí road 8–12 km N of El Llano, 400–450 m, *Nee et al. 8771* (MO, US). E slope of Cerro Jefe in *Clusia* forest, 2700 ft, *Tyson 3390* (MO). Cerro Jefe 0.4 km beyond turnoff to Altos de Pacora, *Witherspoon & Witherspoon 8568* (MO, US).

2. **Drymonia alloplectoides** Hanst., Linnaea 34: 358. 1865. TYPE: Costa Rica, *Warscewicz 34* (B, probably not extant).—FIG. 16.

D. alloplectoides var. *vallicola* Morton, Ann. Missouri Bot. Gard. 29: 54. 1942. TYPE: Panamá, *Woodson & Schery 203* (US, holotype; MO, isotype).

Epiphytic suffrutescent *herbs*, *subshrubs*, *shrubs*, or *lianas*; stems often pendent to repent, to 5 m long, succulent, terete, reddish, and brown hirsute when young, becoming woody, subquadrangular, gray brown and glabrate when mature, the nodes swollen; numerous short branches present. *Leaves* subequal in a pair, opposite, ovate, oblong, or obovate, 3.6–12.9 cm long, 2.5–4.9 cm wide, subcoriaceous, the apex acute to rounded, the base acute to rounded, occasionally oblique, subentire to serrate, dark green above, becoming dark brown when dry from brown hirsute hairs which are more dense at the veins, below lighter green, densely hirsute; petioles 2–12 mm long, brown hirsute. *Inflorescences* near the apices of the short branches or main stems, of single flowers; pedicels 1.0–1.8 cm long, densely hirsute. *Flowers* with a faint sweet odor; calyx all green or all red purple, or green below and red above, or red outside and green within, the lobes bractlike, connate at the base, unequal, 2 anterior lobes broadly elliptic, 2.5–3.0 cm long, the lateral lobes a little shorter, the posterior lobe suborbicular, ca. 1 cm long, the apices obtuse, rounded or acute, serrulate to entire, hirsute especially at the base, the veins prominent; corolla variously colored, white, cream, pink, or purple, with reddish lines, rarely greenish, 4.5–6.5 cm long, oblique in the calyx,

the tube gradually broader from the base, saccate on the upper side at base, spur ca. 0.5 cm long, 0.8 cm wide, hirsute on the upper side, glabrous below, tube ca. 2 cm wide and not contracted at the throat, hirsute outside, puberulent within, the limb somewhat bilabiate, to 3 cm wide, the lobes spreading, suborbiculate, the upper and the lateral lobes 1 cm long and wide, subentire, the lower lobe ca. 1.5 cm long and wide, the lobes fimbriate to erose, often darker colored than the tube; stamens included, the filaments flattened, coiling after anthesis, connate at the base and adnate to the base of the corolla tube, the anthers oblong, ca. 7 mm long with a broad connective, coherent at first, brown; nectary posterior, glabrous; ovary apex grooved, red villous, the style thick, ca. 2.5 cm long, 2–3 mm wide, puberulent, the stigma capitate. *Fruit* a fleshy, red, bivalved capsule surrounded by the accrescent, persistent calyx, valves spreading, exposing the black seeds in the fleshy pulp. *Chromosomes* $n = 9$ (Wiehler, 1972).

This species is common in lowland wet forests in both Costa Rica and Panamá where it clings to the bark of tall trees below the canopy layer.

BOCAS DEL TORO: Farm Six, region of Almirante, *Cooper 472* (US). Changuinola Valley, *Dunlap* (US). Water Valley, *Wedel 969* (MO). Isla Colón, Chiriquí Lagoon, *Wedel 1325* (MO). COCLÉ: La Mesa, El Valle de Antón, 1000 m, *Allen 2569* (MO, US). El Valle, 39 km from Panamerican Highway, *Correa 310* (MO). Road past Furlong's Finca due N of Cerro Pilón, 880 m, *Croat 37511* (MO). Hills above El Valle de Antón, *Dressler 3565* (PMA). Cloud forest on slopes of Cerro Pilón near El Valle, 700–900 m, *Duke 12071* (MO, REED). Foothills of Cerro Pilón near El Valle, 900 m, *Duke & Correa 14654* (MO). Between Cerro Pilón and El Valle, 700–900 m, *Duke & Dwyer 13921* (MO, SCZ). 5 mi N of El Valle de Antón, 1000 m, *Luteyn 1207* (DUKE, MICH, NY). Trail from La Mesa towards Los Llano and border between Coclé and Panamá, *Luteyn 4097* (DUKE). El Valle to La Mesa, 2400–2600 ft, *Spellman et al. 570* (MO). Poor trail to La Mesa ca. 4.5 mi beyond El Valle de Antón, *Wilbur & Luteyn 11673* (DUKE). Near La Mesa 5 mi N of El Valle, *Wilbur & Luteyn 11725* (DUKE, F). North rim of El Valle de Antón near Cerro Turega, 650–700 m, *Woodson & Schery 162, 203* (both MO, US). COLÓN: Zona maderera de Santa Rita, *Correa & Dressler 984* (PMA). Between Nuevo Tonosí and Río Indio on road from Portobelo and Nombre de Dios, near sea level, *Croat 33537* (MO). Río Guanche above bridge on Portobelo Road, 50–200 m, *Croat 37020* (MO). Río Iguanita, 390 m, *Skog et al. 4184* (E, MO, US). DARIÉN: Cerro Pirre, *Duke 6098* (MO). PANAMÁ: Campo Tres 5 km NE of Altos de Pacora, *Busey 817* (DUKE, NY, US, USF). Cerro Campana, *Croat 14210* (MO). El Llano-Cartí Road 7–12 km from Panamerican Highway, 350–400 m, *Croat 25094* (MO). Cerro Campana, *D'Arcy & Dressler 5487* (MO); *Dressler 4018* (PMA). El Llano to Cartí Road, first stream N of Panamerican Highway, *Folsom et al. 1909* (MO, US). El Llano-Cartí Road, 11–18 km from Panamerican Highway, 350 m, *Mori & Kallunki 5126* (MO, US); 400–450 m, *Nee & Tyson 10943* (MO, US); *Skog & Folsom 4168* (MO, P, US). WITHOUT LOCALITY: Western Panamá, *Stork 141* (US).

3. **Drymonia conchocalyx** Hanst., Linnaea 34: 360. 1865. TYPE: Between Desengaño and Cariblanco, Costa Rica, *Wendland 954* (not seen).

D. brevipes Morton, Ann. Missouri Bot. Gard. 29: 54. 1942. TYPE: Panamá, *Allen 2330* (US, holotype).

Epiphytic *shrubs* or *lianas*; stems 1–3 m long, purplish toward the apex or green, glabrous, the nodes sometimes swollen. *Leaves* often unequal or one of a pair

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FIGURE 16. *Drymonia alloplectoides* Hanst. Habit (×½). [After *Nee & Tyson 10943* (MO).]

falling early; blades elongate elliptic or oblong, 9–32 cm long, 4–10 cm wide, coriaceous, the apex acuminate, the base rounded, acute, or oblique, entire, both sides green, glabrous; petiole to 3 cm long, purplish or green, glabrous. *Inflorescences* in the upper leaf axils, 1 or 2 per axil; peduncles and bracts lacking; pedicels 2–4 cm long, reddish, glabrous. *Flowers* showy, the calyx oblique, irregular, the anterior lobes larger, 1.0–3.0 cm long, all connate at the base for 1.0–1.5 cm, ovate or oblong, yellow to purple, glabrous, entire; corolla whitish to purplish, with darker spots or with apparent yellow lines, drying purplish, the tube oblique in the calyx, spurred or saccate at the base, broader toward the limb, not contracted above, to 7 cm long, glabrous, the limb pink to purple, lobes toothed; filaments adnate to corolla tube at the base, flattened, glabrous, the anthers oblong, ca. 6.5 cm long; disc gland 1, thick, glabrous; ovary strigillose, the style glabrous, ca. 4 cm long, the stigma stomatomorphic. *Capsule* yellow to purplish, surrounded by the persistent calyx; seeds not seen.

Drymonia conchocalyx is much more common in Costa Rica, but it has been collected in the provinces of Bocas del Toro, Chiriquí, Coclé and Veraguas in Panamá.

The population occurring on Cerro Pilón in Coclé has been separated as *Drymonia brevipes* Morton, mainly on the basis of the apparently longer connation of the calyx lobes giving the appearance of a 3-lobed calyx, and shorter pedicels. Populations of this species in Costa Rica have similar characters. When specimens over the whole range are examined, *D. brevipes* does not seem to be a distinct species.

BOCAS DEL TORO: Between Criollo, just above Buena Vista, and Quebrada Higuerón on Chiriquí Trail, *Kirkbride & Duke 794* (MO). CHIRIQUÍ: Cerro Colorado on upper mining road 20–28 mi from San Félix, 1200–1500 m, *Croat 33347* (MO). COCLÉ: Slopes of Cerro Pilón near El Valle, 700–900 m, *Duke 12122* (MO, USF). Cerro Pilón, hill below summit, above El Valle de Antón, 2000–2700 ft, *Dwyer et al. 4536* (MO). La Mesa above El Valle, 1000 m, *Gentry 5661* (MO). Cerro Pilón, 900–1173 m, *Liesner 758* (US). Cerro Pilón 5 km NE of El Valle, 800–1045 m, *Mori et al. 6629* (MO). VERAGUAS: N of Santa Fé 11 km from Escuela Agricola Alto de Piedra, *Mori & Kallunki 3085* (MO, US).

4. **Drymonia coriacea** (Oerst. ex Hanst.) Wiehl., Phytologia 27: 325. 1973.

Erythranthus coriaceus Oerst. ex Hanst., Linnaea 26: 209. 1854. TYPE: Turrialva, Costa Rica, *Oersted* (C, holotype, not seen).
Alloplectus coriaceus (Oerst. ex Hanst.) Hanst., Linnaea 34: 363. 1865.
Columnea coriacea (Oerst. ex Hanst.) Kuntze, Rev. Gen. 2: 472. 1891.
Alloplectus ventricosus J. D. Smith, Bot. Gaz. (Crawfordsville) 25: 154. 1898. TYPE: Atirro, Prov. Cartago, Costa Rica, *Smith 6727* (US, holotype, US, US, isotypes).

Epiphytic *shrubs* or suffrutescent *herbs*; stem lax, stout, to 2.5 m tall, green or reddish, strigillose toward the apex, unbranched or flowering branches ascending from the nodes of the prostrate stems. *Leaves* nearly equal to unequal in a pair, elliptic, lanceolate or oblanceolate, sometimes falcate, 8–25 cm long, 4–10 cm wide, coriaceous, the apex acuminate, the base cuneate, entire, reddish and glabrous on both sides or sparsely strigillose below along the prominent veins; petiole 1–5 cm long, reddish purple. *Inflorescences* appearing congested in the upper leaf axils, few flowered; peduncles lacking; bracts nearly enclosing the

flowers, ovate, numerous, persistent, to 1.5 cm long, red purple, strigillose; pedicels ca. 1 cm long, red, strigose. *Flowers* not conspicuous; calyx oblique, the lobes similar to the bracts, unequal, the posterior lobe smaller and surrounding the gibbous corolla base, ovate, ca. 1 cm long, the apex rounded, entire to dentate, reddish or rarely green, strigillose; corolla pale orange to purplish, the tube gibbous at the base, narrowed toward the middle then strongly ventricose or pouched on the lower side before contracting to a narrow throat, 1.7–2.2 cm long, ca. 4 mm wide at the base, ca. 1 cm deep at the pouch, ca. 3 mm wide at the throat, glabrous at the base, pilose above, inside glandular, the lobes of the limb erect, semiorbiculate, ca. 2 mm long, 3 mm wide; stamens included, the filaments adnate to corolla tube for ca. 1 cm above the base, the anthers oblong, to 4 mm long, 2 mm wide; disc gland solitary; ovary puberulent, the style glabrous. *Capsule* globose, surrounded by the persistent bracts and calyx, dehiscing by 2 valves; seeds not seen.

Drymonia coriacea is known from Costa Rica to Peru. It is unusual among the Panamanian species of *Drymonia* in having a strongly ventricose corolla similar to that found in some species of *Nematanthus*.

BOCAS DEL TORO: Cricamola, region of Almirante, *Cooper 207* (NY, US). Río Terebe between Quebrada Treglo and Puerto Palenque, 300–350 ft, *Kirkbride & Duke 524* (MO, NY, REED, SCZ). DARIÉN: Between upper Río Membrillo and Camp 7 on road to San Blas, 100–800 m, *Duke 10907* (MO). VERAGUAS: 5 mi W of Santa Fé on road past Escuela Agricola Alto Piedra, 800–1200 m, *Croat 22985* (US). Río Primero Brazo, 2.5 km beyond Agriculture School Alto Piedra near Santa Fé, 700–750 m, *Croat 25453* (MO, PMA). Valley of Río Dos Bocas 11 km from Escuela Agricola Alto Piedra on road to Calovébora, 450 m, *Croat 27487* (MO). Between Alto Piedra School and Río Calovébora, 1.8 mi beyond school, 500 m, *Croat & Folsom 34100* (MO). Between Escuela Agricola Alto Piedra and continental divide, 650–800 m, *Dressler 4730* (PMA). Base of Cerro Tuti, 6.5 km outside of Santa Fé, *Folsom 3017* (MO). Mountains 3–5 mi N of Santa Fé, 500–1000 m, *Gentry 3020* (MO). NW of Santa Fé 2.6 km from Escuela Agricola Alto de Piedra, *Mori & Kallunki 4743* (MO, US). NW of Santa Fé 11 km from Escuela Agricola Alto de Piedra, 450–550 m, *Mori et al. 3845* (MO). First branch of Río Santa María, road from Santa Fé, *Witherspoon & Dressler 8905* (MO, US).

5. **Drymonia flavida** L. Skog.[13] TYPE: Panamá, *Croat 27245* (PMA, holotype).

Epiphytic *shrubs*; stems reddish purple, sparsely strigose above, 4–6 mm in diam., rooting from the nodes. *Leaves* nearly equal in a pair, lanceolate to oblanceolate or oblong, 4–7 cm long, 1.6–3.2 cm wide, subcoriaceous, the apex acuminate, the base acute to rounded, entire, above and below purplish, sparsely strigillose; petioles 3–10 mm long, purple, strigillose. *Inflorescences* axillary; peduncles short or lacking; bracts lanceolate, 1.0–1.5 cm long, purple, sparsely strigillose; pedicels 1.5 cm long, purple strigose. *Flowers* large, the calyx lobes more or less erect, free to the base, ovate, ca. 4 cm long, 3 cm wide, green tinged, deep red purple, the outside sparsely strigillose, the inside sericeous at the base, the apex acute to acuminate, the base strongly cordate, the margin entire; corolla yellow, immature, fleshy, tubular, ca. 2 cm long, 1 cm in diam., densely sericeous outside, the inside glabrous, the lobes of the limb short, 2 mm long, 3 mm wide;

[13] *Drymonia flavida* L. Skog, sp. nov. *Drymoniae semicordatae* (Poepp.) Wiehl. e Peru affinis bracteis lanceolatis 1.0–1.5 cm longis et brevioris quam calycis lobis, corollis dense sericeis differt.

stamens immature, the filaments curved, glabrous, the anthers coherent by their sides in a group of 4, each ca. 8 mm long, 3 mm wide, yellowish, glabrous, the disc not seen; style reddish, pilose. *Fruit* and seeds not seen.

This species from the province of Darién resembles *Drymonia semicordata* (Poepp.) Wiehl. from Peru. The Peruvian species differs in having large bracts much longer than the short calyx lobes, and a merely strigillose corolla.

DARIÉN: Upper gold mining camp of Tyler Kittredge on headwaters of Río Tuquesa ca. 2 air km from continental divide, *Croat 27245* (PMA).

6. **Drymonia folsomii** L. Skog, Brittonia 30: 321. 1978. TYPE: Panamá, *Folsom et al. 4850* (US, holotype; MO, isotype).

Epiphytic vinelike *subshrubs*; stem woody, slender, 3–5 mm in diam. above, green and glabrous toward the apex, brown below, the internodes to 3 cm long, the nodes prominent. *Leaves* equal to unequal in a pair, ovate or elliptic, 2.3–8.5 cm long, 1.0–3.5 cm wide, membranous, the apex acute to acuminate, the base acute, serrulate, above dark green, strigillose, below lighter green, glabrous; petioles 0.5–2.0 cm long, glabrous or verrucose on drying. *Inflorescences* in the upper axils, 1-flowered; peduncles lacking; bracts minute, linear, 1–2 mm long; pedicels ca. 2 cm long, slender at the base, ca. 1.5 mm in diam., broader toward the apex, to 4 or 5 mm wide, glabrous, but strigillose at the apex. *Flowers* showy; floral tube ca. 1 cm in diam., the calyx somewhat oblique, the lobes ovate or triangular, 0.8–1.1 cm long, 0.5–0.9 cm wide, erect except the upper lobe pushed back by the corolla spur, the basal lobes connate for ca. 8 mm, the upper and the lateral lobes connate ca. 3 mm, the apex acute, the margin serrate, the outside strigose, green and lavender or reddish, the inside strigillose; corolla white with a deep red spot in the throat, the tube oblique in the calyx, funnelform to subcampanulate, 3.0–3.6 cm long, the spur bulbous and fleshy, ca. 5 mm long, the tube 6 mm in diam. just above the spur, suddenly larger at the middle and ampliate to ca. 1.5 cm in diam. at the throat, the outside pilose at the base, becoming strigose above, the inside glandular, densely so on the upper side, the limb oblique, the lobes rotund, the upper 8 mm long, the lower lobe 1.0 cm long, 1.3 cm wide, the margins crenate to erose; stamens included, the filaments broad and fleshy at the base, filiform above, to 1.8 cm long, yellow, glabrous, coiling after pollen is shed, the anthers sagittate, 4 mm long, 2 mm wide; disc reduced to a single ovate posterior gland; ovary narrowly conic, puberulent, the style curved, ca. 1.2 cm long, pilose below, the stigma capitate. *Capsule* elongate globose, 1.0–1.2 cm long, 0.7–0.9 cm wide, dehiscent by 2 fleshy recurving lavender valves; seeds narrowly filiform, 1 mm long, longitudinally striate, dark reddish brown.

Drymonia folsomii has been collected twice on Cerro Colorado in Chiriquí Province and frequently in Costa Rica, growing at mid-elevations in cloud forest.

The species is named for James P. Folsom, who collected this and many other members of the Gesneriaceae in Panamá.

CHIRIQUÍ: Cerro Colorado, 8.8 km from main road, 1450–1750 m, *Folsom et al. 4850* (MO, US). Cerro Colorado, 50 km N of San Félix on the continental divide, 1200–1500 m, *Mori & Dressler 7791* (MO).

7. **Drymonia lanceolata** (Hanst.) Morton, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1173. 1938.

Episcia lanceolata Hanst., Linnaea 34: 346. 1865. TYPE: Cariblanco, Costa Rica, *Wendland 902* (not seen).

Terrestrial *herbs* or *subshrubs*; stems quadrangular, succulent to 2 m tall, green, minutely strigillose toward the apex. *Leaves* opposite, equal in a pair, broadly elliptic, 9.6–34.4 cm long, 4.6–14.4 cm wide, membranous, the apex acuminate, the base cuneate, crenulate, above dark green, sparsely strigose, below lighter green, densely tomentose at the prominent veins, strigose between the veins; petioles elongate, to 14.4 cm long with small stipulelike outgrowths on the stem at the base of the petiole. *Inflorescences* of 1–3 flowers in a cluster per axil; peduncles lacking; bracts linear, ca. 0.5 cm long, green, strigose; pedicels 1–5 cm long, angled, green strigose. *Flowers* showy; calyx somewhat oblique, the lobes unequal, the posterior lobe smaller, all lanceolate to ovate, 2.3–4.6 cm long, 0.7–1.7 cm wide near the cordate base, the apex long acuminate, entire, light green, strigose; corolla white outside, yellow inside and on the lobes, oblique in the calyx, the tube with a short spur and curved, 3.5–4.5 cm long, ca. 1 cm wide above the base, slightly broader above, sparsely strigose, the limb 2-lipped, the basal lobe erect, others spreading, the lobes fimbriate; filaments broad at the base above insertion, glabrous, coiled, the anthers oblong, ca. 5 mm long, curved; disc gland suborbicular, fleshy, thick, ca. 2 mm long; ovary and style puberulent, the stigma deeply bilobed, papillate. *Capsule* ovoid; seeds not seen.

This species has been collected in Costa Rica and in the provinces of Bocas del Toro, Chiriquí, and Veraguas in Panamá. The large, white, fragrant, fringed corolla distinguishes *Drymonia lanceolata* from other terrestrial species of *Drymonia*.

BOCAS DEL TORO: Róbalo Trail, N slopes of Cerro Horqueta, 6000–7000 ft, *Allen 4987* (MO, US). Chiriquicito-Calderas Trail between Quebrada Higuerón and Gutierrez, *Kirkbride & Duke 764* (MO). CHIRIQUÍ: Cerro Horqueta, 7000 ft, *Blum & Dwyer 2590* (FSU, MO, SCZ). Road along ridge, Cerro Colorado last stream before rising to antenna, 1650 m, *Folsom et al. 4775* (MO, US). Boquete region, Cerro Horqueta, 6500 ft, *Hagen & Hagen 2098* (NY), *2123* (NY, US). Between Pinola and Quebrada Hondo toward summit on Chiriquí Trail, *Kirkbride & Duke 884* (MO). N of San Félix at Chiriquí-Bocas del Toro border, 5000–5500 ft, *Mori & Kallunki 5914* (MO, US). Bajo Chorro near Río Caldera, 1900 m, *Skog & D'Arcy 4090* (E, P, MO, US). Quebrada Velo, 1800 m, *Woodson & Schery 268* (MO, US). VERAGUAS: 15–20 km NW of Santa Fé between Escuela Agricola Alto Piedra and continental divide, 650–800 m, *Dressler 4729* (PMA). Base of Cerro Tuti, *Folsom 3019* (MO), *3025* (MO, US). NW of Santa Fé 8.8 km from Escuela Agricola Alto de Piedra on road to Calovébora, 1900 ft, *Mori 6661* (MO). 11 km from Escuela Agricola Alto de Piedra along Río Dos Bocas, *Mori & Kallunki 3167* (MO, US). NW of Santa Fé, 8.8 km from Escuela Agricola Alto de Piedra, *Mori & Kallunki 4856* (MO); *Mori et al. 3922, 3956* (both MO).

8. **Drymonia macrantha** (J. D. Smith) D. Gibson, Phytologia 23: 336. 1972.

Alloplectus macranthus J. D. Smith, Bot. Gaz. (Crawfordsville) 31: 117. 1901. TYPE: Cubilquitz, Alta Verapaz, Guatemala, *Tuerckheim 7642* (US, holotype; US, isotype).
A. tucurriquensis J. D. Smith, Bot. Gaz. (Crawfordsville) 54: 238. 1912. TYPE: Las Vueltas, Tucurrique, Prov. Cartago, Costa Rica, *Tonduz 13042* (US, holotype).

Epiphytic or terrestrial *shrubs*; stems short, the whole plant rarely to 2 m tall, thick, strigillose at least toward the apex. *Leaves* large, broadly ovate to broadly

elliptic, 20–30 cm long, 10–20 cm wide, membranous, the apex acute, the base cuneate and decurrent, dentate or serrate, above dark green, strigose, below lighter green to purplish, strigose especially along the veins; petioles thick. *Inflorescences* of several showy flowers congested in the upper leaf axils; peduncles ca. 5 mm long, the bracts large and leaflike; pedicels ca. 1.5 cm long, puberulent; calyx oblique, the lobes green or becoming reddish or orange, oblong, 2–3 cm long, connate at the base, the apex obtuse, puberulous, entire; corolla white or cream, often yellow within tube and red or purple on the throat, tube horizontal in the calyx, spurred at the base, ventricose above and slightly narrowed at the throat, 3–7 cm long, puberulous, the limb ca. 3 cm across, the lobes unequal with the basal lobe larger and toothed, the upper and the lateral lobes usually entire, orange red; stamens included, the anthers oblong, ca. 5 mm long; ovary strigillose, the stigma stomatomorphic. *Capsule* ovoid to globose surrounded by the persistent calyx, to 1.7 cm long; seeds reddish. *Chromosomes* $n = 9$ (Wiehler, 1972).

Drymonia macrantha is native to Mexico south to Panamá, where it has been collected in the province of Chiriquí in moist forests.

The name *Episcia purpusii* (T. S. Brandegee) T. S. Brandegee cannot be maintained as a synonym of *Drymonia macrantha*. When Brandegee saw material of *Drymonia macrantha*, *Purpus 7216*, he mistakenly believed it to be the same as *Purpus 6857*, the type of *Solenophora purpusii* that he had described earlier. On the strength of this incorrect observation he transferred *S. purpusii* to *Episcia*. But the two Purpus collections are not the same, not even the same genus, thus his synonymy cannot be accepted. Neither can the annotation of *Purpus 7216* as the type of *Episcia purpusii* be accepted because the transfer of the epithet to *Episcia* clearly cites *Solenophora purpusii* as the basionym.

CHIRIQUÍ: Between Concepción and El Hato de Volcán, *D'Arcy 4254B* (MO). Barriles, 6–16 km S of Volcán, 1000–1300 m, *Dressler & Williams 3992* (DUKE, MO, PMA, US). 4.7 km S of Questa Piedra along Concepción-Volcán road, *Folsom 3960* (MO, US). Valley of the upper Río Gariché, 1050–1100 m, *Seibert 362* (MO).

9. **Drymonia macrophylla** (Oerst.) H. E. Moore, Baileya 3: 112. 1955.

Caloplectus macrophyllus Oerst., Cent. Gesn. 45. 1858. TYPE: Naranjo, Costa Rica, *Oersted 9268* (C, holotype; MO, US, photos).
Drymonia mucronulosa Hanst., Linnaea 34: 353. 1865. TYPE: Guatemala, *Sell* (not seen).
Alloplectus macrophyllus (Oerst.) Hemsl. in Godm. & Salv., Biol. Cent.-Am., Bot. 2: 484. 1882.
Columnea macrophylla (Oerst.) Kuntze, Rev. Gen. 2: 472. 1891.
Drymonia ochroleuca Standl., Field Mus. Nat. Hist., Bot. Ser. 12: 413. 1936, non Poepp. TYPE: Temash River, British Honduras, *Schipp S901* (F, holotype, not seen).
D. belizensis Standl., Trop. Woods 52: 29. 1937. TYPE: Based on *D. ochroleuca* Standl.
D. rosea Morton, Ann. Missouri Bot. Gard. 29: 56. 1942. TYPE: Panamá, *Allen 2489* (US, holotype; US, isotype).

Terrestrial or epiphytic *herbs* or *shrubs* or rarely *vines*; stem lax or erect, to 1.5 m tall, to 1 cm thick, subquadrangular, strigillose to glabrate. *Leaves* equal to unequal in a pair, elliptic, ovate, oblong, or oblanceolate, sometimes falcate, 8.2–35 cm long, 3.5–14 cm wide, membranous to subcoriaceous, the apex acute

to acuminate, the base cuneate or acute, sometimes unequal, denticulate to crenate or serrulate, above green, strigillose to scabrous, below light green or reddish, especially between the veins, strigillose, the veins prominent; petioles thick, 1–5 cm long, strigillose. *Inflorescences* in the upper leaf axils, 1–few flowered; peduncles lacking; bracts small; pedicels short, less than 1 cm long. *Flowers* with calyx lobes thin, subequal, ovate, 1.0–1.5(–2.8) cm long, green, or with red veins, or all red, strigillose, the margin comblike, fimbriate, dentate or serrate, the apex sometimes mucronate; corolla pale yellow or cream, usually more yellow inside and with a red or purple area on the lower surface in the throat, the tube waxy with a short spur, ampliate toward the limb, not contracted above, 3–6 cm long, densely puberulent outside, the inside glabrous or glandular, the limb of rounded lobes spreading, ca. 0.5 cm long, the lower lobe longer, minutely toothed; stamens included, the filaments adnate to the base of the corolla tube, glabrous, later coiling, the anthers 3–5 mm long, at first coherent, after anthesis separating; disc gland thick, glabrous; ovary nearly glabrous to pubescent, green, the style white, puberulent, the stigma stomatomorphic. *Chromosomes* $2n = 18$ (Lee, 1962).

Drymonia macrophylla is known from Guatemala to Peru, although first described from Costa Rica.

As in many other widely distributed species in the Gesneriaceae, *Drymonia macrophylla* is variable, especially in leaf coloration. Corolla length seems quite variable, also. Two specimens (*Foster & Kennedy 1858* (DUKE); *Liesner 1223* (US)) from Panamá Province have mature corollas reaching 6 cm long. In other characters the specimens are similar to other specimens of the species from nearby localities. Most specimens have corollas ca. 3 cm long, but occasionally some plants bear corollas 4 or 5 cm long.

Dried specimens often resemble *Alloplectus ichthyoderma*, but that species can be distinguished by the scaly stem epidermis, by the shorter and more pilose corollas, and location at higher elevations in Chiriquí Province where *Drymonia macrophylla* is as yet unknown.

BOCAS DEL TORO: Top of second fila above Almirante, *Gentry 2811* (MO). Old Bank Island, Chiriquí Lagoon, *Wedel 2124* (MO, US). Without other locality, *Wedel 484* (MO). COCLÉ: Hills N of El Valle de Antón, 800 m, *Dressler 4236* (PMA). Slope of Cerro Pilón near El Valle, 700–900 m, *Duke 12144* (MO). Foothills of Cerro Pilón near El Valle, 900 m, *Duke & Correa 14658* (MO). Foot of Cerro Pilón near El Valle, 2500 ft, *Dwyer & Correa 7973* (MO). La Mesa, 2200 ft, *Dwyer & Nee 11950* (MO). 3 km NE of El Valle, *Mori & Kallunki 2954* (MO, US). La Mesa above El Valle, 800 m, *Skog & Butcher 4124* (US). COLÓN: Between Nuevo Tonosí and Río Indio on road from Portebelo and Nombre de Dios, near sea level, *Croat 33547* (MO). Santa Rita Ridge trail, 17–35 km from Boyd-Roosevelt Highway, 400–800 m, *Mori & Crosby 6356* (MO). Río Guanche, ca. 3–4 km above bridge on road to Portobelo, *Witherspoon & Witherspoon 8661* (MO). PANAMÁ: Road from El Llano to Cartí-Tupile, 12 mi above Panamerican Highway, 200–500 m, *Croat 22849* (US). Campo Tres beyond Cerro Jefe, 700 m, *Croat 27054* (MO). 1 mi upstream from Frizzel's Finca Indio, slopes of Cerro Jefe, *Foster & Kennedy 1858* (DUKE). El Llano Cartí-Tupile road 11–18 km above Panamerican Highway, 200–600 m, *Liesner 1223* (US); *Skog & Folsom 4174* (E, MO, US). VERAGUAS: Valley of Río Dos Bocas, 11 km from Escuela Agricola Alto Piedra on road to Calovébora, 450 m, *Croat 27561* (MO). Third branch of Río Santa María 12–15 km NW of Santa Fé, 650–750 m, *Dressler 4995* (PMA). Lower slopes Cerro Tute ca. 10 km NW of Santa Fé, 750–1000 m, *Mori et al. 7546* (MO). NW of Santa Fé, 11 km from Escuela Agricola Alto de Piedra, 450–550 m, *Mori et al. 3844* (MO).

10. **Drymonia multiflora** (Oerst. ex Hanst.) Wiehl., Phytologia 27: 325. 1973.

Calanthus multiflorus Oerst. ex Hanst., Linnaea 26: 208. 1854. TYPE: Naranjo, Costa Rica, *Oersted* (C, holotype, not seen).
Alloplectus multiflorus (Oerst. ex Hanst.) Hanst., Linnaea 34: 361. 1865.
Columnea multiflora (Oerst. ex Hanst.) Kuntze, Rev. Gen. 2: 472. 1891.

Epiphytic *vines* or *shrubs;* stems slender, to 1 m, the internodes short, brittle, strigillose, branched. *Leaves* equal to greatly unequal in a pair, lanceolate to elliptic, 2.2–9.7 cm long, 0.7–3.4 cm wide, subcoriaceous when fresh, the apex acuminate, the base cuneate to rounded, subentire to serrate, above dark green, shiny, glabrous, below lighter green, minutely strigillose; petiole 0–6 mm long. *Inflorescences* axillary, of single flowers; peduncles lacking; bracts minute; pedicels 0.7–1.0 cm long, red, strigillose. *Flowers* few; calyx not oblique, the lobes nearly equal, ovate, 0.8–1.5 cm long, the apex acuminate, deeply toothed, green to purplish, usually red; corolla white to yellow with reddish stripes in the tube, or purplish within or on the limb, the tube erect in the calyx, with a short rounded spur at the base, ca. 2.5 cm long, slender, ventricose above, then contracted at the throat, glabrous below, sparsely pilose above outside, the limb somewhat 2-lipped, the lobes small, nearly entire to erose, ciliate; anthers oblong; ovary globose, reddish, pilose. *Capsule* surrounded by the persistent calyx, globose, ca. 0.8 cm in diam., dark red to nearly black; seeds oblong, ca. 1 mm long, reddish brown, lined, but not noticeably twisted.

This species is known from Costa Rica and the Atlantic slope in Panamá.

BOCAS DEL TORO: Above Quebrada Huron on Cerro Bonyik, 150–260 m, *Kirkbride & Duke* 592 (MO, REED, SCZ). Fish Creek Mountains, Chiriquí Lagoon, *Wedel* 2337 (MO). COCLÉ: Rivera's sawmill, Alto Calvario, 700–900 m, *Folsom 3214* (MO). El Copé, El Petroso, *Folsom & Lantz 1886B* (MO, US). PANAMÁ: Gorgas Memorial Labs yellow fever research camp ca. 25 km NE of Cerro Azul on Río Piedras, 550 m, *Barrett et al. 3436* (MO). VERAGUAS: Río Primero Brazo 2.5 km beyond Agriculture School Alto Piedra near Santa Fé, 700–750 m, *Croat 25466* (MO). 8.8 km from Escuela Agricola Alto de Piedra, *Mori & Kallunki 3228* (MO).

11. **Drymonia parviflora** Hanst., Linnaea 34: 352. 1865. TYPE: Candelaria, Costa Rica, *C. Hoffman* (not seen).

Epiphytic *herbs*, *subshrubs* or *shrubs*; stems stout, subquadrangular, the internodes somewhat verrucose, tomentose, the nodes swollen. *Leaves* often strongly unequal; blades elliptic, falcate, 6–20 cm long, 3–9 cm wide, membranous, the apex acute to acuminate, the base cuneate or decurrent, the margin shallowly dentate, above dark green, occasionally with paler veins, strigillose, below paler green, often reddish, pubescent; petioles often elongate, 0.5–4.0 cm long. *Inflorescences* of few to several flowers congested in the upper leaf axils, the pedicels strigillose; calyx lobes pale pink to purplish, ovate, 1.5–2.5 cm long, ca. 1.5 cm wide at the base, serrate, sparsely strigose; corolla yellow, not much longer than the calyx, the tube slightly curved, broader toward the limb, sparsely pilose outside, the limb spreading, the lobes erose; ovary pilose. *Capsule* ovoid, surrounded by the persistent calyx, ca. 8 mm long, purplish, pubescent; seeds oblong, dark brown, longitudinally striate, embedded in black matrix.

Drymonia parviflora resembles *D. macrantha* in habit but the leaves and

flowers are smaller in this species. Originally described from Costa Rica, *D. parviflora* can be found in Panamá in the province of Chiriquí.

CHIRIQUÍ: Bajo Mono-Róbalo trail, W slopes of Cerro Horqueta, 5000–7000 ft, *Allen 4786* (MO, US). Las Lagunas, 2 km SE of Volcán, 1300 m, *Dressler 7156* (MO, PMA). Ridge road at Cerro Colorado 4.3 km from main road, 1450–1750 m, *Folsom et al. 4803* (MO, US). Bajo Mono and Quebrada Chiquero, 1500 m, *Woodson & Schery 566* (MO, US).

12. **Drymonia rubra** Morton, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1175. 1938. TYPE: Yerba Buena, Prov. Heredia, Costa Rica, *Standley & Valerio 49933* (US, holotype).

Terrestrial or epiphytic *shrubs* or *lianas*; stem lax, succulent when young, becoming woody, to 2 m tall, subterete to quadrangular, strigillose at the apex, glabrescent below. *Leaves* often unequal in a pair, elliptic to obovate, 6.8–20.2 cm long, 2.8–8.8 cm wide, subcoriaceous, the apex acuminate, the base cuneate, entire, above dark green, sparsely strigillose, below lighter green or reddish, sparsely strigillose; petioles 1–4 cm long. *Inflorescences* axillary, of 1 or few flowers; peduncles lacking; bracts linear, strigillose; pedicels 0.5–5 cm long, strigillose. *Flowers* showy; calyx large, oblique, the lobes lanceolate to ovate, 3.5–5.0 cm long, 1.1–2.8 cm wide, the apex acuminate, the base rounded or cordate, subentire, green to creamy white, glabrous; corolla dark red, or with longitudinal light streaks or white at the base, a band of red at the middle and lighter toward the limb, or with a yellow area on the lower limb, oblique in the calyx, the tube curved, broader above from a gibbous or a saccate base, not contracted at the limb, 3–6 cm long, strigillose outside, the limb spreading, the lobes suborbicular, erose; anthers oblong, ca. 5 mm long; ovary strigillose. *Capsule* ovoid, 1.5–2.0 cm long, 1.2 cm wide, white at maturity; seeds not seen.

Drymonia rubra was originally described from Costa Rica, but is now known from the provinces of Bocas del Toro, Chiriquí, Coclé, Colón and Veraguas in Panamá.

BOCAS DEL TORO: Fish Creek Mountains, Chiriquí Lagoon, *Wedel 2359* (MO, US). CHIRIQUÍ: Between Pinola and Quebrada Hondo toward summit on Chiriquí Trail, *Kirkbride & Duke 883* (MO). COCLÉ: Hills S of El Valle, 2500 m, *Allen 4379* (MO). La Mesa 4 km N of El Valle, 850 m, *Nee & Dwyer 9190* (MO, US). COLÓN: Lower Río Guanche, *Dressler 4928* (PMA). VERAGUAS: Valley of Río Dos Bocas between Escuela Agrícola Alto Piedra and Calovébora, 15.6 km NW of Santa Fé, 450–550 m, *Croat 27655* (MO). 10 km NW of Santa Fé on road to Calovébora, at first branch of Río Santa María, *Mori & Bolten 7633* (MO). 11 km from Escuela Agrícola Alto de Piedra along Río Dos Bocas, *Mori & Kallunki 3142* (MO, US). NW of Santa Fé 1 km from Escuela Agrícola Alto de Piedra on slopes of Cerro Tute, *Mori & Kallunki 4796* (MO). NW of Santa Fé, 8.8 km from Escuela Agrícola Alto de Piedra, *Mori & Kallunki 6187* (MO). NW of Santa Fé 11 km from Escuela Agrícola Alto de Piedra, in valley of Río Dos Bocas, 450–550 m, *Mori et al. 3836, 3862* (both MO). 7 km W of Santa Fé past agricultural school, 2900 ft, *Nee 11241* (MO, US).

13. **Drymonia serrulata** (Jacq.) Mart., Nov. Gen. 3: 59, 1829 & 3: 192. 1832.

Besleria serrulata Jacq., Hort. Schönbr. 3: 21, *tab. 290*. 1798. TYPE: Cult., Hort. Schönbrunn, *Jacquin* (W, not seen).

B. spectabilis Kunth, in H.B.K., Nov. Gen. Sp. Pl. 2: fol. ed. 321; qto. ed. 400. 1818. TYPE: Smita R., between La Sequia and Popayan, Dept. Cauca, Colombia, *Humboldt & Bonpland 2028* (P-BO, not seen; IDC 6209–2, 58. II, 7).

Drymonia bicolor Lindl., Bot. Reg. 24: *tab. 4.* 1838. Illegitimate renaming of *Besleria serrulata* Jacq.
D. jacquinii G. Don., Gen. Hist. 4: 653. 1838. Based on *Besleria serrulata* Jacq.
D. spectabilis (Kunth) Mart. ex G. Don, Gen. Hist. 4: 653. 1838.
D. cristata Miq., Linnaea 18: 26. 1844. TYPE: Surinam, *Focke 766* (U, not seen).
D. parvifolia Griseb., Fl. Brit. W.I. 463. 1861, not Morton. TYPE: Magdelena, Santa Marta, Colombia, *Purdie 177* (GOET, K, not seen).
D. maculata S. Moore, Trans. Linn. Soc. London, Bot. Ser. 2, 4: 410. 1895. TYPE: Barro do Bugres, Matto Grosso, Brazil, *S. Moore 529* (BM, not seen).
D. chiapensis T. S. Brandeg., Univ. Calif. Publ. Bot. 6: 64. 1914. TYPE: Finca Mexiquito, Chiapas, Mexico, *Purpus 6875* (UC, holotype, not seen).

Succulent, terrestrial *herbs* or low *shrubs*, epiphytic or scandent *shrubs*, or more usually *lianas*; stem succulent when young, becoming woody with a papery bark, when erect to 2 m tall, or to 10 m long and 10 cm in diam. near the base when climbing, often with adventitious roots in the internodes or with prominent brownish corky lenticels on woody stems, reddish or green, sparsely strigose or puberulous toward the apex; branched or not. *Leaves* opposite, equal to nearly equal in a pair, elliptic or oblong to obovate, 4–19 cm long, 2–8 cm wide, the apex acute or acuminate, the base cuneate to rounded, sometimes oblique, serrulate to sinuate dentate, somewhat succulent when fresh, dark green or with a lighter patterning above, sparsely strigillose to scabrous, below light green to purplish or with a purple patterning especially in younger leaves, sparsely strigillose to glabrescent, less between the veins; petioles 0.6–30 cm long, appressed pubescent. *Inflorescences* of solitary or rarely to 3 flowers in the leaf axils; peduncles, lacking; pedicels 0.5–2.5 cm long, puberulous. *Flowers* large and showy; calyx of 5 more or less free leaflike lobes, the 4 lobes erect, nearly equal, ovate, lanceolate to oblong, decurved, 2–5 cm long, 0.5–3 cm wide, acute or acuminate at the apex, the base rounded to cordate, the fifth (dorsal) calyx lobe smaller than the others and curved around the corolla spur, all with entire, sinuate to serrulate margins, puberulous or sparsely strigillose on both sides, persistent and accrescent in fruit; corolla variously colored, from white, cream, pale yellow, pink, dark red to purple, often with red, lavender, maroon, or purple veins or spots in the throat of the tube, coloring becoming darker during anthesis, 3–7 cm long, puberulent outside, inside glandular pubescent at least toward the throat, the tube oblique, with a basal globose spur, then contracted above the spur, gibbous or ventricose dorsally above, then broadening toward the throat, 2–3 cm long, 3–8 mm wide at the base, 10–20 mm wide at the throat; limb broad, bilabiate, the lobes rounded, 1.0–1.5 cm wide, serrulate, reflexed, except the lower anterior lobe which is larger and erose fimbriate, all often darker colored or spotted; stamens included, held in the throat at anthesis, then coiling and withdrawing, the filaments broader at the base, glabrous, the anthers connivent, ca. 6 mm long, 2 mm wide, the base spurred and sagittate, the staminode small, glabrous; disc of a single large gland or annular and dorsally widened, glabrous; ovary ovoid, puberulous, the style elongating as filaments withdraw, ca. 2.5 cm long, curved, glandular pubescent; stigma bilobed. *Capsule* globose to broadly ovoid, 1–2 cm long and wide, puberulous, the line of dehiscence prominent, bivalved, the valves thick and fleshy, yellowish to purplish

outside, orange to red within with a large dark conic mass of placental and funicle tissue and seeds; seeds black, shiny, oblong, fusiform, ca. 1 mm long, twisted and striate. *Chromosomes* $2n = 18$ (Ratter, 1963), $n = 9$ (Wiehler, 1972).

Drymonia serrulata is the most widely distributed species in the genus and one of the most widely distributed of the Gesneriaceae. It is found from México to the Matto Grosso in Brazil, and on the Lesser Antilles. Its habit and habitat are equally as diverse: it is sometimes an epiphyte, but often rooted in the ground and climbing on trees or shrubs; it sometimes grows over rocks on exposed limestone outcrops, beaches or sea-cliffs or in moist undisturbed forests, and it even occurs in dry-deciduous woods, at roadsides, clearings, and second growth forests. In Panamá it has been widely collected at low to middle elevations except in lowlands of Chiriquí Province.

A population from Cerro Jefe appears to be intermediate between *Drymonia serrulata* and *D. alloplectoides* in leaf size and serration, and in flower size and color. The plant(s) may be the result of hybridization between the two commonly collected parents that are both found in Panamá Province, on or near Cerro Jefe.

BOCAS DEL TORO: Changuinola valley, *Dunlap 217* (US), *555* (US). Chiriquí Lagoon, *Wedel 1219*, (MO, US), *1245* (US), *1272*, *1388* (all MO, US), *1281* (MO). Water Valley, Chiriquí Lagoon, *Wedel 1555* (MO, US). Old Bank Island, Chiriquí Lagoon, *Wedel 1890*, *2006*, *2052* (all MO, US). Little Bocas, Chiriquí Lagoon, *Wedel 2497* (MO, US). Shepherd Island, Chiriquí Lagoon, *Wedel 2708* (MO, US). CANAL ZONE: Barro Colorado Island, *Aviles 54a* (MO); *Bangham 415* (US); *Bartlett & Lasser 16730* (MICH, MO); *Croat 6037* (DUKE, F, MO, NY); *Croat 6054* (F, MO, SCZ); *Croat 6121* (MO, NY, SCZ); *Croat 6130* (MO); *Croat 6153* (MO, SCZ); *Croat 7332* (F, MO, NY, SCZ); *Croat 11737* (MO, NY, SCZ, US); *Croat 11756* (MO, SCZ); *Croat 11771* (MO); *Dwyer 1443* (MO, SCZ, US); *Ebinger 269* (F, MO); *Kenoyer 541* (US); *Killip 40024* (US); *Shattuck 143*, *294*, *508*, *1065* (all MO); *Standley 41135* (US); *Weaver & Foster 1474* (DUKE, F, MO, PMA); *Wilbur & Weaver 10787* (DUKE); *Woodworth & Vestal 371* (MO). TTC Albrook Tower, *Blum 1079* (MO, SCZ). Road S-10, N of Escobal, *Croat 12438* (MO, MO). Forest N of Summit Hills Golf Course, *Croat 16654* (MO). Espave forest along Albrook-Ft. Clayton dump road, *Duke & Mussell 6625* (MO, US). Fort Sherman, *Dwyer 7184* (MO, NY). Coco Solo, U.S. Army Tropic Test Center, Mine Emplacement Center, *Dwyer & Duke 7886* (MO). Roadside woods, Madden Dam, Boy Scout Camp Road, *Dwyer & Elias 7501* (MO). Madden Dam, *Ebinger 846* (MO, US). Pipeline Road, *Gentry 1424* (MO). Road K-19, 2 mi from W border of Zone to cleared area near Canal, *Gentry 1788* (MO, NY, SCZ). Coco Solo, *Gentry 6073* (MO). Cerro Galera ca. 2 km from Pacific Ocean near W boundary of Canal Zone, 350–400 m, *Gentry 6638* (MO). Madden Dam, 50 ft, *Lewis et al. 5* (MO). U.S. Naval Ammunition Depot 2 mi W of Balboa on Highway 1, *Luteyn & Foster 924* (DUKE). NW corner of Zone on inland road to Pinas from Gatún, 80 m, *Mori & Kallunki 1939* (MO, PMA). RR and Panama Canal 6 km W of Gamboa, 30–40 m, *Nee 7205* (MO). ½ km W of Gamboa, 30 m, *Nee 7501* (MO, US). Fort Sherman near mouth of Chagres River, *Tyson 1531* (FSU, MO, SCZ). Old Fort San Lorenzo, *Tyson 1579* (FSU, MO, SCZ, US), *2231* (FSU, MO, SCZ). Between Fort Davis and Coco Solo Hospital, *Tyson 6810* (MO, NA, PMA). CHIRIQUÍ: Boquete, 3800 ft, *Davidson 828* (MO, US). S of Questa Piedra along Concepción-Volcán road, *Folsom 3961* (MO, US), *3962* (MO, US). COCLÉ: El Valle de Antón, N Hills, *Allen 3557* (MO, US); *Bartlett & Lasser 16707* (MICH, MO). 8 mi N of El Valle de Antón, *Luteyn & Kennedy 1708* (DUKE, MICH, MO). W slope and summit of Cerro Valle Chiquito, 700–800 m, *Seibert 499* (MO). N slopes of Cerro Guacamayo, SE of El Valle, 1800 ft, *Webster 16860* (MO). Between Las Margaritas and El Valle, *Woodson et al. 1765* (MO, NA, US). COLÓN: Orillas de Río Boquerón, ca. 3 km de la Pelona, *Carrasquilla et al. 391* (MO). 2 mi NE from Puerto Pilón, trail along Río Piedras, *Correa & Haines 252* (DUKE, MO, PMA). Coastline between Garotte and La Guaira, *D'Arcy 9357* (MO). Hills just N of Río Guanche, *Davidse & D'Arcy 10066* (MO). Thickets near

beach, Maria Chiquita, E of Río Piedras toward Portobelo, *Dwyer & Kirkbride 7776* (MO). Between Río Piedras and Puerto Pilón, *Lewis et al. 3223A* (MO, SCZ). 6 mi SW of Portobelo, *Luteyn 1428* (DUKE). Tributary of Quebrada Anchca 4 km E of Buena Vista, 3 km N of cement plant, 80 m, *Nee 7782* (MO, US). Fató (Nombre de Dios), sea level, *Pittier 3843* (US). Río Sirrí, Trinidad Basin, 20–50 m, *Pittier 4017* (US). Santa Isabel, sea level, *Pittier 4180* (US). DARIÉN: Peak ca. 300 ft high between Río Balso & Río Aretí at their confluence, *Duke 8732* (MO, REED). Quebrada Maskia off Río Pucro above Pucro, *Duke 13089* (MO, OS). Quebrada Bidoto (Peccary Creek) off Río Aretí, *Duke 13595* (MO). Río Tuira, between Río Punusa & Río Mangle, *Duke 14606* (MO, REED). Camino del Pirre, *Duke & Bristan 256* (MO). River Canglon, *Duke & Bristan 379* (MO). Puerto Saint Dorotea, on beach, *Dwyer 2273* (MO). Río Tuquesa, at middle Tuquesa Mining Company camp called Charco Peje, 250 m, *Mori 7022* (MO). Caná, 1750 ft, *Stern et al. 462* (MO, US). Penas Bay near hotel, *Tyson 5526* (DUKE, FSU, MO). LOS SANTOS: Loma Prieta, 800–900 m, *Duke 11857* (MO, REED), *11872* (MO, OS). Cerro Pilón, 2700 ft, *Dwyer & Lallathin 8622* (MO). Loma Prieta, Cerro Grande, 2400–2800 ft, *Lewis et al. 2221* (MO, SCZ). N of Guaniquito, ca. 10 mi N of Tonosí along Río Tonosí, 100–200 m, *Luteyn & Foster 1374* (DUKE). PANAMÁ: Cerro Jefe, *Dressler 3575* (PMA); *Dwyer & Gauger 7382* (MO). Río Chagres, 1 mi above Madden Lake, *Duke 4477* (MO, US). Río Pita, 0–2 mi above tidal limit, *Duke 4791* (MO, US). Chepo Highway W of Río Pacora, *Duke 5889* (MO). Cerro Campana, *Duke 5987* (MO). San José Island, road between Bodega Bay and Mata Pierco, *Duke 12530* (MO). Between Cañasas and Sábalo, 100 m, *Duke 14486* (MO). Alhajuela, *Dwyer 1139* (SCZ). Goofy Lake to 1.5 mi S of Goofy Lake, 1800 ft, *Dwyer & Hayden 8034* (MO). Goofy Lake toward Cerro Azul, ca. 2 mi S of Goofy Lake, *Dwyer & Stimson 8068, 8073* (both MO). San José Island, Pearl Archipelago, Main Beach, *Harlow 53* (US). Main Beach, San José Island, *Johnston 62* (MO, US). Region of Cerro Azul, Finca El Indio, ca. 0.5 mi in, 750 m, *Kennedy 1527* (MO). Path beyond the village of La Eneida, 1000 m, *Luteyn & Foster 1108* (DUKE). Ridge 3 km S of Alcalde Diaz, 410–440 m, *Nee 8560* (MO). Alhajuela, *Paul 497* (US). Chepo, 60 m, *Pittier 4467* (US). 1 mi E of El Llano, *Tyson 6838* (MO, NA, PMA). SAN BLAS: Beach E of Puerto Obaldía, *Croat 16904* (MO). Nakka, *Dwyer 6885* (MO, SCZ). WITHOUT LOCALITY: *Hayes 827* (NY).

14. **Drymonia stenophylla** (J. D. Smith) H. E. Moore, Baileya 3: 112. 1955.

Alloplectus stenophyllus J. D. Smith, Bot. Gaz. (Crawfordsville) 25: 153. 1898. TYPE: Forests of Suerre, Llanuras de Santa Clara, Costa Rica, *J. D. Smith 6724* (US, holotype, not seen).
Drymonia parvifolia Morton, Ann. Missouri Bot. Gard. 29: 56. 1942, not *D. parvifolia* Griseb. TYPE: Panamá, *Allen 1949* (MO, holotype).
D. mortoniana Wiehl., Phytologia 27: 325. 1973, based on *D. parvifolia* Morton.

Epiphytic *shrubs*; stems erect, 0.3–0.5 m long, strigillose only at the apex, glabrescent below. *Leaves* nearly equal to strongly unequal in a pair, lanceolate to elliptic, 5–13 cm long, 1.1–4.2 cm wide, subcoriaceous, the apex acuminate, the base acute to cuneate, entire, above dark green, glabrous or strigillose (Panamá), below lighter green with darker veins, glabrescent. *Inflorescences* in the upper leaf axils of 1 or 2 flowers; peduncles lacking; bracts reduced or lacking, pedicels slender, 0.5–1.5 cm long, glabrous; calyx oblique, the lobes unequal, lanceolate to ovate, 0.8–1.7 cm long, the apex acute, entire or rarely serrulate, or with prominent vein endings, green or rarely reddish, glabrous; corolla white, the throat yellow or pink, the limb white or reddish, the tube oblique in the calyx, the spurred base slender, ca. 3 mm in diam., broader above, to 1 cm wide, 2–3 cm long, the lobes of the limb erose to shortly fimbriate; stamens included, the filaments coiling after anthesis, glabrous; anthers oblong; disc gland single, thick, glabrous; ovary oblong, pubescent at the apex and the base of the style; stigma stomatomorphic. *Capsule* enclosed in persistent calyx; seeds not seen. *Chromosomes* $n = 9$ (Lee, 1962).

Drymonia stenophylla is more common at low to middle elevations in Costa

Rica, from where it was first described. In Panamá it can be found at somewhat higher altitudes in Chiriquí Province. The width of the calyx lobes, the corolla color and leaf size vary throughout the range, but the species holds together in characters of size and shape of corolla, ovary pubescence, as well as in other characters.

Drymonia aciculata is a similar species but differs in having red-streaked corolla lobes.

CHIRIQUÍ: Trail from San Félix to Cerro Flor, 100–850 m, *Allen 1949* (MO). SW slope of Volcán Barú, 5000 ft, *Butcher* (US). NW side of Cerro Pando, *Croat 15945* (MO, NY, USF). Cerro Fortuna, 1400–1600 m, *Dressler 5392* (PMA). Road 3–5 mi NW of El Hato del Volcán towards Costa Rica across the Río Chiriquí Viejo, 3000–4000 ft, *Luteyn 855* (DUKE). COLÓN: Hills N of El Valle de Antón, trail to La Mesa, 1000 m, *Allen 2691* (US, US). Mountains beyond La Pintada, 400–600 m, *Hunter & Allen 550* (MO).

15. **Drymonia sulphurea** Wiehl., Selbyana 2: 109. 1977. TYPE: Cerro Jefe, Prov. Panamá, Panamá, *Wiehler & Dressler 71213* (SEL, holotype, not available for study).

Terrestrial or epiphytic *herbs* or *subshrubs*; stems erect, quadrangular, succulent, to 30 cm tall, ca. 1 cm wide, green to reddish, the upper part of the stem strigillose, the internodes to 5.5 cm long, the nodes swollen. *Leaves* nearly equal in a pair, ovate, elliptic to obovate, 7.9–24.8 cm long, 3.4–14.0 cm wide, fleshy when fresh, membranous when dry, the apex acuminate, the base acute to rounded, crenulate, above bullate, dark green, glossy, glabrous, below red to purple, strigillose, the veins prominent; petioles stout, 1.6–8.4 cm long, 2–3 mm wide when dry, reddish, strigillose. *Inflorescences* in the upper leaf axils, short racemose, of 4–10 flowers; peduncles 2–6 mm long, strigillose; bracts reddish; pedicels slender, 1.1–3.1 cm long, strigillose. *Flowers* with the calyx lobes ovate, ca. 2 cm long, pale green, strigillose on both sides, the apex acute to rounded, the base cordate, entire; corolla horizontal in the calyx, the tube saccate at the base, puberulent or strigose outside, broadening toward the throat, pale green to yellow or cream, glandular inside, 2–3 cm long, ca. 1 cm wide at the throat limb with the upper and lateral lobes reflexed, ca. 5 mm long, subentire, the basal lobe erect, slightly longer, erose; stamens included, filaments ca. 2 cm long, adnate to the base of the corolla tube, glabrous above; anthers ca. 4 mm long; disc gland dorsal, white, glabrous, the ovary pubescent, the style glandular pubescent, the stigma broadly bilobed. *Fruit* unknown.

Drymonia sulphurea is closely related to *D. turrialvae* Hanst. and may be a local variant of the latter widespread species. Examination of the type, which was not available, may show that *D. sulphurea* should be reduced to a subspecies or variety. *Drymonia turrialvae* differs in the red to purple calyx lobes, the broader stigma, and apparently shorter corolla. *Drymonia sulphurea* is known only from the area near Cerro Jefe in the province of Panamá.

PANAMÁ: La Eneida, region of Cerro Jefe, *Dressler 3648* (US). Road between Cerro Jefe and La Eneida, *Luteyn & Foster 1137* (DUKE). Woods around La Eneida, 1000 m, *Luteyn & Kennedy 1771* (DUKE).

16. **Drymonia turrialvae** Hanst., Linnaea 34: 359. 1865. TYPE: In Volcano Turrialva, Costa Rica, *Wendland 517*, 952 (syntypes not seen).

D. marmorata Hook. f., Bot. Mag. 110: *tab. 6763*. 1884. TYPE: Cult., Kew Gardens (K, holotype, not seen).

Terrestrial or epiphytic *herbs* or low *shrubs*; stems succulent, quadrangular, to 0.5 m tall, stout, red to purple, becoming pale brown, strigillose to glabrous, unbranched. *Leaves* equal in a pair, fleshy, ovate to suborbicular, large, 8.7–29.5 cm long, 3.9–25.4 cm wide, membranous when dry, the apex acuminate to cuspidate or rounded, the base rounded or cordate, crenulate to subentire, above bullate, glossy dark green, glabrous, the veins sunken, below pink to red or purple, puberulent at least on the veins to glabrous, the veins prominent; petioles often long, stout, sometimes scaly, 2.3–21.7 cm long, 2–6 mm wide, purplish. *Inflorescences* in the upper axils, flowers many in congested racemes; peduncles ascending, short, red; bracts oblong, red purple, puberulent; pedicels to 4 cm long, red purple, glabrescent. *Flowers* showy; calyx lobes ovate, shiny, red purple, 1–3 cm long, puberulent, entire or inconspicuously toothed; corolla lilac, pink, cream, light yellow or white with yellow on the limb, the tube horizontal in the calyx, saccate at the base, puberulent, broader toward the throat and not contracted above, waxy, to 6 cm long, the limb bilabiate, the lobes rounded, the lower lobe larger and fimbriate; stamens included, the filaments shortly adnate to the base of the corolla tube, flattened, coiled after anthesis, the anthers oblong, ca. 5 mm long; disc gland broadly triangular, yellow, glabrous; ovary reddish, glabrous, the style yellow, puberulent; style scoop shaped. *Fruit* a fleshy capsule, oblate or globose, lavender, blue, pink, red to purple, ca. 1 cm in diam.; seeds fusiform, reddish, striate.

Drymonia turrialvae often inhabits dark, damp openings near waterfalls or streams, occupying a site where the plants are in the spray from the falls or stream as water runs over rocks. In the dark humid atmosphere the leaves can become large and dark colored, and the light colored corolla makes a striking contrast to the purplish calyx, bracts, and leaves.

This species is known from Costa Rica and Panamá, but also has been collected as far south as Ecuador.

BOCAS DEL TORO: Buena Vista, region of Almirante, *Cooper 223* (NY). Quebrada Huron, 300–400 ft, *Kirkbride & Duke 434* (MO). Between Buena Vista coffee finca and Cerro Pilón on Chiriquí trail, *Kirkbride & Duke 684* (MO, NY, REED, REED). Fish Creek Mountains, Chiriquí Lagoon, *Wedel 2306* (MO, US). CHIRIQUÍ: W side of Cerro Pando, 6000 ft, *D'Arcy & D'Arcy 6659* (F, MO). Waterfall near road between Río Sereno and Volcán, *Skog et al. 4019* (E, MO, P, US). COCLÉ: Hills N of El Valle de Antón, trail to La Mesa, 1000 m, *Allen 2696* (US). Cerro Gaital Caracoral, 2700–3200 ft, *Dwyer & Correa 8864* (MO). La Mesa, 650–710 m, *Mori et al. 1907* (MO). El Petroso at Rivera's sawmill, 7 km beyond El Copé, 800 m, *Skog et al. 4201* (US). DARIÉN: Cerro Pirre, *Bristan 551* (MO, OS). Ascent of Cerro Pirre from Río Pirre S of El Real, 750–1030 m, *Duke 5343* (MICH, MO). Cerro Pirre, *Duke 6082* (MICH). Rancho Río, Cerro Pirre, W slope, 2200 ft, *Duke 6605* (MO). Elfin forest, Cerro Campamiento, S of Cerro Pirre, *Duke 15661* (US). Cerro Pirre, 2500–4500 ft, *Duke & Elias 13773* (MO), *13776* (NY), *13816* (MO). Cerro Pirre, between Pirre and next southern peak, *Folsom 4377* (MO), *4379B* (US). Summit of Cerro Pirre, 1000 m, *Gentry 4604* (MO). Summit of Cerro Pirre, 1000–1400 m, *Gentry & Clewell 6954* (MO, SCZ). Cerro Mali on Colombian border, N slope, 1400–1500 m, *Gentry & Mori 13810* (MO). 0–2 mi E of Tres Bocas along shortest headwater of Río Cuasí, *Kirkbride & Duke 1164* (MO). N slopes of Cerro Pirre, 700–950 m,

Mori & Kallunki 5500 (MO). Cerro de Garagará, Sambú basin, 500–974 m, *Pittier 5671* (US). Caná-Cuasí Trail, Chepigana District, 1200 m, *Terry 1421* (MO). VERAGUAS: Río Primero Brazo 2.5 km beyond Agriculture School Alto Piedra near Santa Fé, 700–750 m, *Croat 25474* (MO). Valley of Río Dos Bocas on road between Alto Piedra and Calovébora, 350–400 m, *Croat 27411* (MO). Valley of Río Dos Bocas 11 km from Escuela Agricola Alto Piedra on road to Calovébora, 450 m, *Croat 27543* (MO, PMA). 15–20 km NW of Santa Fé between Escuela Agricola Alto Piedra and Continental Divide, 650–800 m, *Dressler 4728* (F, MO, PMA). 3.9–5 mi N of Santa Fé, 500–1000 m, *Gentry 29883* (MO, SCZ). N of Santa Fé, ca. 2 km N of Escuela Agricola Alto de Piedra, *Mori & Kallunki 2631* (MO). 6–7 km W of Santa Fé on road past agriculture school, 2900 ft, *Nee 9754* (MO). Near 2nd branch of Río Santa María, road from Santa Fé, *Witherspoon & Dressler 8894* (MO).

17. **Drymonia variegata** Uribe, Mutisia 11: 1. 1952. TYPE: Al NE de la poblacion en el paraje "Paramitos," Mun. de Nariño, Depto. Antioquia, Colombia, *Uribe 2144* (COL, holotype; COL, isotype).

Epiphytic vinelike *herbs* or *shrubs*; stems more than 0.5 m long, slender, 3–5 mm in diam., the internodes 1–6 cm long, green to reddish, pilose, sericeous or villous toward the apex, the nodes thicker; branches short. *Leaves* opposite, lanceolate, ovate to oblong, 8–11 cm long, 3.5–4.6 cm wide, membranous, the apex acuminate, the base rounded oblique, crenulate, above dark green to bronze with silvery veins, bullate, pilose, below red violet, villous especially along the veins; petioles 1.1–1.7 cm long, reddish, villous. *Inflorescences* axillary, single flowered; peduncles and bracts not seen; pedicels ca. 1 cm long, reddish, pilose. *Flowers* showy; calyx lobes unequal, free to the base, slightly spreading, the dorsal lobe smaller, oblong, ca. 8 mm long, ca. 2 mm wide, the other lobes 1.0–1.2 cm long, ca. 3 mm wide, green toward the base, reddish toward the acute apex, the margin toothed above, pilose outside and toward the apex inside; corolla "cream with magenta markings at the base of the lobes," (fide Gentry & Clewell) the tube slender, ca. 3 cm long, ca. 5 mm in diam. at the spurred base, above ca. 9 mm in diam., outside pilose, above inside glabrous, the lobes fimbriate; stamens (in bud) with lower filaments adnate to the base of the corolla tube ca. 5 mm, slender, the upper fialments free almost to the base, broad, all glabrous, the anthers ca. 5 mm long, sagittate; disc reduced to a single dorsal gland; ovary ovoid, ca. 6 mm long, densely pilose, the style glandular puberulent, the stigma broadly stomatomorphic to bilobed. *Fruit* interior red, seed mass purple.

This species is known from Colombia and in Panamá near the summit of Cerro Pirre in Darién Province. *Drymonia variegata* is distinctive from the species it resembles most closely, *Drymonia* species A, from western and Central Panamá, by the bullate leaves.

DARIÉN: Cerro Pirre, valley between Pirre and next most southerly peak, *Folsom 4425* (MO, US). Summit of Cerro Pirre, 1000–1400 m, *Gentry & Clewell 6992* (PMA).

18. **Drymonia warscewicziana** Hanst., Linnaea 34: 352. 1865. TYPES: Costa Rica, *Warszewicz 17, 28* (not seen).—FIG. 17.

Terrestrial or more usually epiphytic *herbs*, *shrubs*, or *lianas*; stems succulent, 1–2 m tall, nearly glabrous. *Leaves* opposite, nearly equal in a pair, narrowly or broadly elliptic to obovate, 4.6–15.2 cm long, 1.8–7.6 cm wide, membranous, the

Figure 17. *Drymonia warszewicziana* Hanst.—A. Habit (×⅜). [After *Skog et al. 4199* (MO).]—B. Fruit (×⅜). [After *Duke & Dwyer 13918* (MO).]

apex acuminate, the base cuneate, acute, sometimes oblique, nearly entire, above dark green, glabrous, below lighter green or reddish, sparsely strigillose; petioles slender, 0.7–3.1 cm long, green or reddish, sparsely strigillose. *Inflorescences* axillary of 1 or 2 flowers; peduncles lacking; bracts linear, 2–3 mm long, the pedicels ca. 1 cm long, glabrous. *Flowers* with the calyx lobes oblique, unequal, lanceolate or narrowly ovate, 1.4–2.7 cm long, 6–10 mm wide, light green or green with dark red or darker green veins, or completely maroon, glabrous, long acuminate, the base rounded to cordate, sparsely pubescent to glabrous, entire but ciliate; corolla infundibuliform, the tube white or cream outside, reddish inside, glabrous below, strigose toward the limb, curved, oblique in the calyx, 2–3 cm long, ca. 5 mm in diam. at the saccate base, 8–10 mm in diam. at the throat, the limb spreading, oblique, the lobes rotund, each 5–7 mm long, reddish, lavender or yellow, erose; filaments coiling after anthesis, the anthers oblong,

ca. 4 mm long; ovary pubescent; style puberulous toward the base, glabrescent above. *Fruit* flattened, ovoid, ca. 1 cm long, greenish outside, opening into 2 valves, inside brownish purple; seeds broadly fusiform, dark reddish brown, striate.

Drymonia warscewicziana is usually epiphytic in trees or growing over rocks in wet forests at elevations usually less than 1,000 m. It ranges from Costa Rica to northern South America. In Panamá the species is found mainly on the Atlantic slope from Bocas del Toro to Darién.

BOCAS DEL TORO: Between Buena Vista coffee finca and Cerro Pilón on Chiriquí trail, *Kirkbride & Duke 708* (MO, REED). COCLÉ: Region N of El Valle, 1000 m, *Allen 3697* (MO, US, US). La Mesa above El Valle de Antón, *Croat 14392* (MO). N slope and summit of Cerro Pilón, 900–1173 m, *Croat 22929* (MO). Between Cerro Pilón and El Valle de Antón, 700–900 m, *Duke & Dwyer 13918* (MO, SCZ). Cerro Pilón above El Valle de Antón, 2000–2700 ft, *Dwyer et al. 4548* (MO, SCZ), *4572* (MO). Above El Valle, 1000 m, *Gentry 5685* (MO). La Mesa N of El Valle, 1000 m, *Gentry 6843* (MO). Hills above El Valle, *Gentry 6878* (MO). 5 mi NW of El Valle de Antón, 1000 m, *Luteyn 1228* (DUKE, MO). El Petroso at Rivera's sawmill, 7 km beyond El Copé, 800 m, *Skog et al. 4199* (E, MO, P, US). La Mesa above El Valle de Antón, 1000 m, *Weaver & Foster 1632* (DUKE). COLÓN: Río Guanche above bridge on Portobelo Road, ca. 3–5 km above bridge, 50–200 m, *Croat 36961* (MO). Old logging road above Río Iguanita, 390 m, *Skog et al. 4187* (E, MO, P, PMA, US). DARIÉN: Cuasí-Caná trail between Cerro Campamiento and La Escalera to "Paramo" E of Tres Bocas, *Kirkbride & Duke 1333* (MO, NY). VERAGUAS: 5 mi W of Santa Fé on road past Escuela Agrícola Alto Piedra, 800–1200 m, *Croat 22994* (MO, DUKE). Road between Escuela Agrícola Alto Piedra above Santa Fé and Río Dos Bocas, ca. 10 km from the Escuela, 530–620 m, *Croat 25885* (MO). Road between Escuela Agrícola and Alto Piedra and Río Dos Bocas ca. 5–8 km from Escuela, 730–770 m, *Croat 25968* (MO). Valley of Río Dos Bocas along road between Escuela Agrícola Alto Piedra and Calovébora, 15.6 km NW of Santa Fé, 450–550 m, *Croat 27770* (MO). Guabal, Río Dos Bocas, 16 km NW of Santa Fé, 500 m, *Dressler 4788* (PMA). Above Río Primero Brazo, 5 mi NW of Santa Fé, 700–1200 m, *Liesner 987* (MO, NA, NY, NY). 8–11 km from Escuela Agrícola Alto de Piedra along Río Dos Bocas, *Mori & Kallunki 3091*, *Mori & Kallunki 4855* (both MO, US); 450–550 m, *Mori et al. 3849*, *Mori et al. 3975* (both MO).

19. **Drymonia** species A.*

Epiphytic *lianas*; stems rooting at the nodes and climbing on trees, slender, internodes elongated up to 10 cm long, 3.5 mm in diam., green or reddish, densely pilose toward the apex, sparse below; occasionally branched. *Leaves* subequal in a pair, elliptic, ovate to oblong, 3.5–8.5 cm long, 1.5–4.5 cm wide, membranous, the apex acute to acuminate, the base subcordate to acute, dentate crenate, above light or dark green to purplish, appressed pilose, below green to deep purple, appressed pilose; petioles 0.6–2.0 cm long, pilose to villous. *Inflorescences* of single flowers in the upper axils; peduncles lacking; bracts lanceolate, 1 cm long, pilose; pedicels 1.0–1.8 cm long, green, villous with reddish trichomes. *Flowers* showy; calyx lobes erect, broadly ovate, 1.6–2.5 cm long, 1.4–1.9 cm wide at the middle, the apex acute, the base cordate, serrate, sometimes recurved, pale green to red, appressed pilose, more dense along the midvein; corolla white or reddish outside, the inside red with white lines in the throat and at the limb margin, oblique in the calyx, the tube nearly

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* *Drymonia* species A = *D. pilifera* Wiehl., Selbyana 5: 82, 1978.

straight, 3.5 cm long, the base spurred on the upper side, 5–7 mm in diam. at the base, slightly arcuate at the middle, ca. 8–10 mm in diam. at the throat, the outside pilose, the inside glabrous below but puberulent above, the lobes spreading, orbiculate, ca. 7 mm long and wide, erose; stamens included, the filaments adnate to the lower side of the corolla for 1 cm, free on the upper side, total length ca. 2.8 cm long, glabrous, coiled after pollen shed, the anthers oblong, hardly sagittate, locules parallel, 2–3 mm long, coherent by their apices; disc reduced to a single acute dorsal gland, reddish; ovary ovoid, ca. 6 mm long, reddish, pilose, the style curved, ca. 1.7 cm long, reddish, glabrous, the stigma broadly stomatomorphic to bilobed. *Capsule* fleshy, surrounded by the accrescent calyx lobes, dehiscent in 2 broad valves, light red outside, purple within; seeds numerous in a blue-black fleshy mass, each ellipsoid, obliquely striate, dark reddish brown.

This species grows in rain forest or cloud forest at low to middle elevations in Costa Rica, and in Panamá in the provinces of Bocas del Toro, Coclé, and Veraguas.

BOCAS DEL TORO: Between Quebrada Menaco and Buena Vista on Chiriquí Trail, transition between premontane rain forest and cloud forest, *Kirkbride & Duke 675* (MO, REED), *676* (MO). COCLÉ: 7 km N of El Copé de Veraguas near Rivera sawmill, Alto Calvario, 900–1300 m, *Folsom 1246* (MO, US); *Folsom 1340* (US), *Folsom 4102* (MO); *Folsom & Lantz 1879*, *Skog et al. 4193* (both US). VERAGUAS: Valley of Río Dos Bocas, 11 km from Escuela Agricola Alto Piedra on road to Calovébora, 450 m, *Croat 27511* (MO). Guabal, Río Dos Bocas 16 km NW of Santa Fé, 500 m, *Dressler 4786* (PMA). 10 km NW of Santa Fé on road to Calovébora, *Mori & Bolten 7638* (MO, US). N of Santa Fé ca. 2–4.2 km N of Escuela Agricola Alto de Piedra, *Mori & Kallunki 2594, 4817* (both MO).

11. EPISCIA

Episcia Mart., Nov. Gen. 3: 39. 1829. TYPE: *E. reptans* Mart.

Alsobia Hanst., Linnaea 26: 207. 1854. TYPE: A. *punctata* (Lindl.) Hanst. = *Episcia punctata* (Lindl.) Hanst.
Cyrtodeira Hanst., Linnaea 26: 207. 1854. TYPE: *C. cupreata* (Hook.) Hanst. = *Episcia cupreata* (Hook.) Hanst.

Stoloniferous low terrestrial or epiphytic *herbs*, rarely suffrutescent; stems decumbent, creeping, or sprawling on the ground or fallen trees, to 1 m or more long, rooting at the nodes, branched or not, pubescent to pilose. *Leaves* often crowded, opposite, usually nearly equal, ovate or elliptic to lanceolate, the upper surface dark green or with various patterns of variegation, the lower surface often colored, the apex acute to rounded, the base acute to cordate; petioles short. *Inflorescences* often of single or 2–6 axillary flowers on slender pilose peduncles, bibracteate. *Flowers* zygomorphic, showy; floral tube short; calyx often irregular, the posterior lobe forced back around the corolla spur, the sepals 5, free or shortly connate at the base, linear, oblong to lanceolate, the apex acute, acuminate or erose, green or colored, pilose; corolla salverform to campanulate, conspicuously spurred, inserted horizontally in the calyx, tubular, white, yellow, blue, purple to red, contracted above the spur and at the throat, rarely ventricose, the limb oblique, 5-lobed, spreading, the lobes rounded, entire, minutely toothed

or fimbriate; stamens 4, didynamous, included, the filaments nearly straight, inserted at the base of the corolla, after anthesis depressed or coiling, the anthers orbicular or oblong, coherent in pairs in a square or arc, becoming free, dehiscing by a longitudinal slit; disc gland 1, large, dorsal, at the base of the ovary; ovary superior, the style included, the stigma stomatomorphic, bilobed, capitate; placentas ovuliferous on both the surfaces or only on the inner surface. *Fruit* an ovoid bivalved fleshy capsule; seeds ellipsoid, shiny, obliquely striate, brown.

Literature:

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a. Corolla limb red or orange red, the tube with a prominent swelling just below the throat, not laterally compressed ..... 1. *E. cupreata*
aa. Corolla limb lavender to white, tube gradually ampliate to the laterally compressed throat ..... 2. *E. lilacina*

1. **Episcia cupreata** (Hook.) Hanst.,[14] Linnaea 34: 340. 1865.

Achimenes cupreata Hook., Bot. Mag. 73: *tab. 4312*. 1847. TYPE: Magdalena, near Soná, Colombia, *Purdie 470* (K, not seen; photo US).
Cyrtodeira cupreata (Hook.) Hanst., Linnaea 26: 207, 215, *pl. 2, fig. 39*. 1853.

Stoloniferous creeping terrestrial *herbs* 5–20 cm tall; stems slender and terete, ca. 5 mm in diam., hirsute, the young stems reddish, the stolons to 50 cm long, reddish or green, hirsute with few branches. *Leaves* grouped at the apex of stolon or branch, equal or subequal in a pair, somewhat bullate, broadly elliptic to oblong ovate, 2.6–8.9 cm long, 1.1–5.0 cm wide, membranous, the apex acute, obtuse or acuminate, the base obliquely rounded to acute or subcordate, crenate to serrate, above dark green, reddish green or with pale green or silvery variegation along the impressed main veins, hirsute, trichomes erect or appressed, below lighter green with prominent veins, the petioles 0.7–4.1 cm long, usually reddish, hirsute. *Inflorescences* of 1–4 flowers; peduncles short, 1–2 mm long, bibracteate; pedicels 1.1–4.5 cm long, reddish, hirsute. *Flowers* showy, usually red; floral tube short, rounded, hirsute; sepals lanceolate, slightly connate at base, 4 sepals erect, the fifth curved around corolla spur, 5–12 mm long, 1–3 mm wide, sparsely pilose, the apex acute, subentire, the outside green or reddish, the inside green; corolla scarlet, bright red, orange, at least on the upper side, yellow and sometimes spotted on the lower side, or rarely all yellow, inside yellow with red or purple spots, the throat with colorless papillae, limb orange

[14] Other synonyms are given by Moore, African Violets, Gloxinias, and Their Relatives, p. 275–276. 1957.

red or deep red, tube ca. 2.0 cm long, 3–4 mm wide at the oblique base, slightly contracted above the spur, above curved and 6–9 mm wide, widening to a prominent swelling just below the throat, the outside villous; spur obtuse, the limb somewhat oblique, 14–25 mm wide, the lobes nearly equal, rounded, entire to erose, the upper lobes somewhat reflexed, the lower lobes spreading; stamens included, the filaments connate at the base, glabrous, contorted after anthesis, the anthers coherent in a square, each orbicular or oblong, staminode ca. 1 mm long, glabrous with a sterile anther; nectary a single glabrous gland, entire or slightly bilobed, rarely 2 lateral glands; ovary ovoid, 2.5–4 mm long, hirsute, the style glabrate, the stigma bilobed. *Capsule* globose, 4–6 mm in diam., hirsute; seeds ellipsoid, ca. 0.5 mm long or less, dark brown.

Episcia cupreata is native to Colombia, Venezuela and Brazil, but is widely grown as a house plant in temperate and tropical areas. In tropical areas where the minimum temperature allows its growth, this species can be used as a ground cover and may escape from cultivation. In Panamá, *E. cupreata* is so far only known from cultivation or as an escape. Cultivars of this species include some found in Panamá: *Episcia* 'Tropical Topaz' with yellow corollas, and another called the Canal Zone Yellow Episcia. Commonly the species is known as the "Flame Violet," but this name may also be applied to *E. reptans* Mart. and to all Episcias.

CANAL ZONE: Powell Garden, Balboa, *Standley 28560, 41192* (both US). PANAMÁ: Borders of lake at Las Cumbres, *Duke 11821* (MO).

2. **Episcia lilacina** Hanst., Linnaea 34: 342. 1865. TYPE: Río Serepigue, near San Miguel, Costa Rica, *Wendland* 782 (B, not seen).—FIG. 18.

Cyrtodeira chontalensis Seem., Gard. Chron. 27: 655. 1867. TYPE: Plants originally collected by Griffin in Nicaragua, described from cultivated material grown at Chelsea (not seen).
Episcia chontalensis (Seem.) Hook. f., Bot. Mag. 97: *tab.* 5925. 1871.
E. fendleriana Kuntze, Rev. Gen. 2: 473. 1891. TYPE: Panamá, *Fendler* 322 (MO, isotype).
E. acaulis J. D. Smith, Bot. Gaz. (Crawfordsville) 61: 378. 1916. TYPE: At the edge of Río de Las Vueltas, Tucurrique, Prov. Cartago, Costa Rica, *Tonduz 13167* (US, holotype; US, isotype).

Prostrate or decumbent terrestrial *herbs* often forming large spreading colonies from stolons; stems succulent, usually short, seldom to 20 cm tall, stout, terete, green to dark red purple, hirsute with spreading hairs, rooting at the nodes. *Leaves* opposite, oblong ovate or elliptic oblong, 3–14 cm long, 1.5–9.0 cm wide, the apex broadly acute or obtuse, the base cordate to acute, occasionally oblique, crenate dentate, above bullate to areolate, dark green or reddish green usually with lighter green near the impressed veins, hirsute, below usually red purple, sometimes light green, pilose; petioles slender, subsulcate, 0.6–2.1(–5.0) cm long, pilose to hirsute with spreading hairs. *Inflorescences* cymose, of 1–6 flowers in the leaf axils; peduncles short when present; bracts 2, lanceolate to spathulate, to 1 cm long, green; pedicels 0.8–2.5 cm long, pilose. *Flowers* showy; floral tube short; calyx of 4 erect anterior sepals 0.8–1.1 cm long, 2–3 mm wide, 1 posterior sepal curved around the spur, slightly shorter and narrower, all

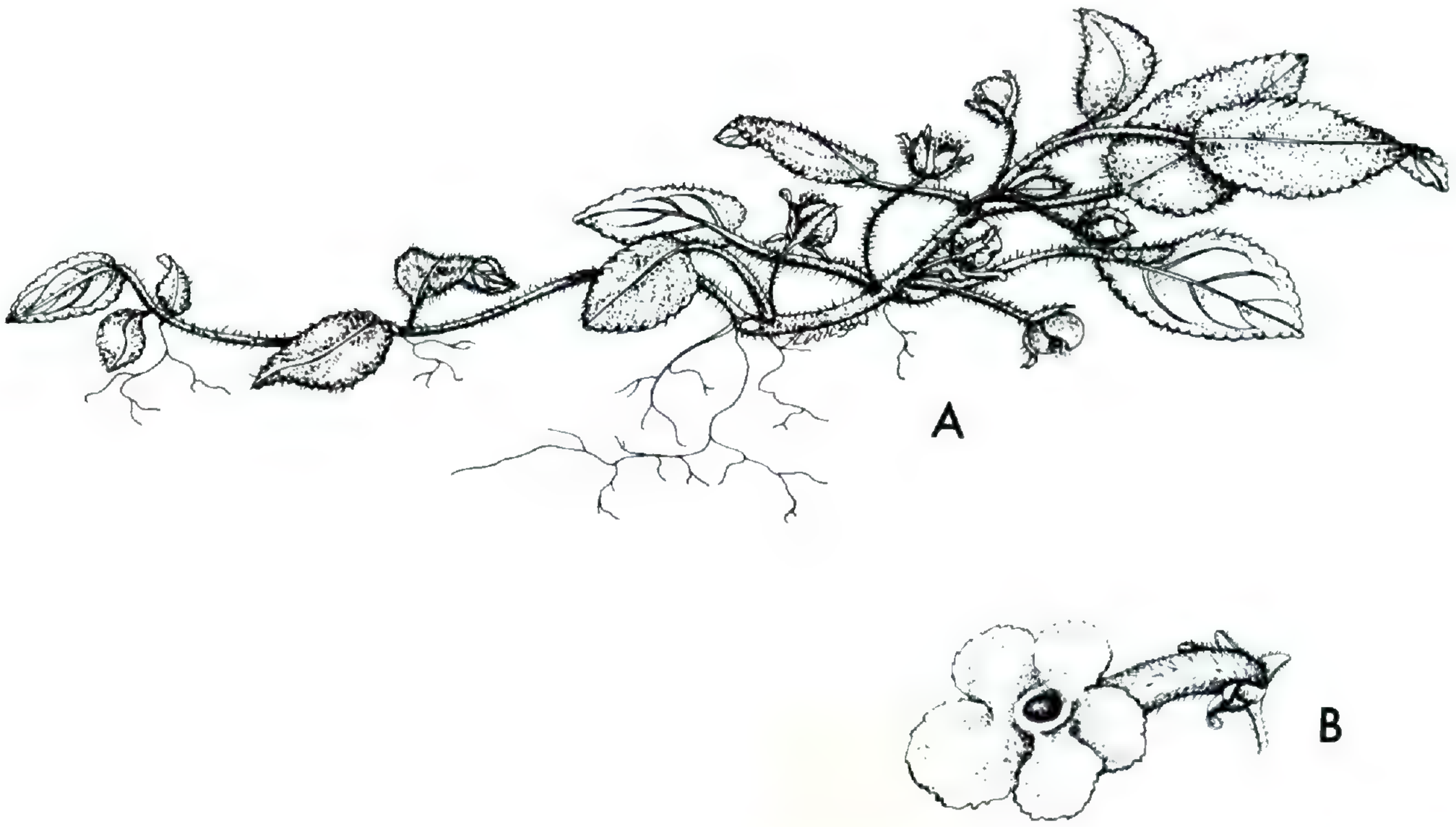

FIGURE 18. *Episcia lilacina* Hanst.—A. Habit with stolons (×½). [After *Skog & Folsom 4176* (MO).]—B. Flower (×⅘). [After *Nee 9283* (MO).]

spathulate, green to reddish purple, pilose, the apex entire to dentate, somewhat recurved; corolla tube white to pale lavender outside, the inside yellow in the throat, white to purple on the limb, the tube 2.0–3.5 cm long, the base 4–7 mm wide, with a rounded spur ca. 5 mm long on the upper side at the base, gradually wider toward the narrow laterally compressed throat which then broadens to a flat subbilabiate limb, the outside pilose, the inside a band of translucent papillae on the upper side to the base of the 2 upper lobes of the limb, the oblique limb composed of 5 orbiculate lobes, to 3 cm wide, 1.5–2.0 cm long, 1.3–1.6 cm wide, denticulate; stamens adnate to base of the corolla for up to 5 mm, the filaments connate for a short distance above the adnation before becoming separate, glabrous, the anthers at first coherent, oblong, 2 mm long, 1.5 mm wide, glabrous, the filaments coiled after anthesis; disc gland 1, emarginate, ca. 1 mm long, yellow, glabrous; ovary apex conic, 3–5 mm long, pilose, the style curved, reaching the corolla throat, nearly glabrous, the stigma capitate. *Capsule* fleshy, globose, ca. 8 mm in diam., pilose; seeds ellipsoid, ca. 0.5 mm long, obliquely striate, reddish brown, shiny. *Chromosomes* $2n = 18$ (Rogers, 1954).

Although *Episcia lilacina* was originally described from Costa Rica, it is much more common in Panamá, particularly in the provinces along the Caribbean coast. The northern limit of the species is in Nicaragua, and to the south *E. lilacina* reaches Chocó and Antioquia in Colombia.

In Panamá *Episcia lilacina* is found at low elevation in tropical and premontane wet forest, usually in shade, occasionally in full sun but in damp locations. It forms large colonies.

Many cultivars are available in the horticultural trade, including one called

'Panamá' for a selection of *Episcia lilacina* from Panamá with unusually narrow dark green leaves.

The only common names known in Panamá for *Episcia lilacina* are "Nepano" from Darién (*Duke 5429*), and "Nappa tuttu purwikua" from San Blas (*Stier 212*). Duke (*14623*, OS) reports that a tea is made of the leaves and "given to snakebite patients when they are hemorrhaging at the mouth."

BOCAS DEL TORO: Cocoa plantation between Almirante and Ojo de Agua 3–6 km W of Almirante, 30–200 m, *Croat 38221* (MO). Chiriquicita to 5 mi S along Río Guarumo, *Lewis et al. 2059* (MO, NY, REED, US). Cocoa plantation 5 km from Almirante along road to Changuinola, 100 m, *Skog & D'Arcy 4159* (US). Fish Creek Mts., Chiriquí Lagoon, *Wedel 2329* (MO, US). Water Valley, Chiriquí Lagoon, *Wedel 790, 1456* (both MO, US), *1607* (MO). CANAL ZONE: Trail from Casa Larga to Río Indio, Madden Dam, *Allen 2359* (US). Mohinga swamp, *Bailey & Bailey 586* (BH). Pipeline Road near Gamboa, *Clewell & Tyson 3208* (MO, SCZ). Pipeline road, 3 mi from Gamboa gate, *Croat 12384* (MO). Banks of Quebrada La Palma and Cañon of Río Chagres, 70–80 m, *Dodge & Allen 17403* (MO, US). Chagres, *Fendler 322* (MO). Near Piña, 0–100 m, *Gentry 8730* (MO, MO). Pipeline Road between 0–3.5 mi NW of Gamboa, *Lewis & Sharp 11* (MO). Pipeline Road, *Smith & Smith 3299* (F, MO, PH, US), *3306* (F, US). Hills N of Frijoles, *Standley 27563* (US). Near Peluca Hydrographic Station, 70 m, *Steyermark & Allen 17254* (MO, US). Trail towards Chico from Indio station to S-49 marker, 3.3 mi from station, *Steyermark & Allen 17438* (MO, US). Cañon of Río Chagres between Quebrada Pura and Río Indio, 70–80 m, *Steyermark & Allen 17509* (MO, US). COLÓN: Camp Pina, 25 m, *Allen 3579* (F, MO, NY, US, US). 9 mi S of Portobelo, *Croat 11382* (F, MO). Santa Rita Ridge, *Croat 13878, 15310* (both MO). Portobelo, *Ebinger 1143* (F, MO, US). Road from Colón to Portobelo, Río Guanche, *Folsom 3765* (MO, US). Santa Rita Ridge, 4–5 mi from Transisthmian Highway, *Gentry 1875* (F, MO, NY, SCZ). Forests around Portobelo, 5–200 m, *Maxon 5790* (F, US). Near Río Boqueron on trail (old road) to Boqueron Mine #2 N of Peluca Hydrographic Station, *Mori & Kallunki 2424* (MO). Santa Rita Ridge, ca. 10 mi from highway, *Porter et al. 4767* (MICH, MO). Santa Rita Ridge ca. 7 mi from Transisthmian Highway, 650 ft, *Wilbur et al. 15053* (DUKE). DARIÉN: Headwater of Río Tuquesa ca. 2 km air distance from Continental Divide, upper gold mining camp of Tyler Kittredge, *Croat 27144* (MO). Ascent of Serrania de Pirre above Caná Gold Mine between Río Caná and Río Escucha Ruido, 600–1000 m, *Croat 37695* (MO). Río Pirre near crossing of trail from El Real to Tucutí, 20 mi W of El Real, *Duke 5186* (MO, PMA). 10 mi S of El Real on Río Pirre, *Duke 5429* (MO). Río Tuira between Río Punusa and Río Mangle, *Duke 14623* (MO, OS). Demartaganala, summit camp, *Duke 15832* (OS, OS). Puerto Sta. Dorothea, *Dwyer 2298A* (MO). Near Cerro Pirre base camp on Río Perrecénega, 200–500 m, *Gentry & Clewell 7052* (MO). Slopes of Cerro Chucula, drainage of Río Pavarandó, *Gentry 4259* (MO). Río Tuquesa at middle Tuquesa Mining Company camp called Charco Peje, 250 m, *Mori 7031A* (MO). Camp Summit, adjacent Darién-San Blas border along Sea Level Canal Route 17, 1000–1200 ft, *Oliver et al. 3678* (MO). Foothills of Garagará, Sambú basin, 30–500 m, *Pittier 5594* (US). Río Paya, trail from Paya to Pucro, *Stern et al. 399* (MO). Río Paya between Paya and Boca de Paya, *Stern et al. 441* (MO, US). PANAMÁ: Cerro Jefe, 900 m, *Correa et al. 1812* (F, MO, PMA). Finca Indio, Cerro Jefe, *D'Arcy & D'Arcy 6234* (MO, NY). Cerro Jefe, *D'Arcy & D'Arcy 6254* (MO). El Llano-Cartí Road, 9–12 km from Panamerican Highway, *D'Arcy 10639* (MO). Between Cerro Azul and Cerro Jefe, *Foster 1152* (DUKE). Majé, 5 mi up the Río Nuevo, a main branch of the Río Majé to the E, *Foster & Kennedy 1994* (DUKE). Finca Indio slopes of Cerro Jefe, *Gentry 2155* (PMA). Caná, 600 m, *Goldman 1886* (US). Tapia River, 75 m, *Killip 3159* (MO). Sandy and rocky river banks, tributary of Río Chagres, 5 mi SW of Cerro Brewster, 1000 ft, *Lewis et al. 3399* (MO), *3402* (DUKE, MO, SCZ), *3403* (MO, SCZ). 10 mi N of highway towards Cerro Jefe, *Luteyn 1327* (DUKE, MO). Gorgas Memorial Labs yellow fever research camp ca. 25 km NE of Cerro Azul on Río Piedras, near fork in river, 550 m, *Mori & Kallunki 3474* (MO). 6.5 km by road N of Lago Azul, 650–730 m, *Nee 9283* (MO). Junction of Río Corso to headwaters of Río Corso, *Oliver 2361* (MO). Upper Mammoní River, 150–400 m, *Pittier 4472* (US). 500 m del restaurante de Cerro Azul, *Reece 7* (DUKE, MO, PMA). Llano-Cartí road, 11.2 km from El Llano and junction with Panamerican Highway, 600 m, *Skog & Folsom 4176* (E, MO, P, US). SAN BLAS: SE of Puerto Obaldía, *Croat 16807* (MO). Trail E of Cangandí-Mandinga airport road 2–5 mi S of Mandinga airport, *Duke 14796* (MO,

US). Río Amila ca. 10 km WSW of Puerto Obaldía, *Mori et al. 6810* (MO). Niatuppu, *Stier 212* (MO). VERAGUAS: Coiba, 50–100 ft, *Collenette 463* (US).

12. GASTERANTHUS*

Gasteranthus Benth., Pl. Hartw. 233. 1846. TYPE: *G. quitensis* Benth.

Besleria L., subgenus *Gasteranthus* (Benth.) Hanst., Linnaea 34: 334. 1865.
Besleria L., sect. *Gasteranthus* (Benth.) Benth. in Benth. & Hook. f., Gen. Pl. 2: 1015. 1876.
Halphophyllum Mansf., Repert. Spec. Nov. Regni Veg. 41: 145. 1937. TYPE: *H. crispum* Mansf. = *Gasteranthus crispus* (Mansf.) Wiehl.
Besleria L., sect. *Neobesleria* Morton, Contr. U.S. Natl. Herb. 26(9): 414. 1939. TYPE: *B. corallina* Fritsch = *Gasteranthus corallinus* (Fritsch) Wiehl.

Terrestrial or rarely epiphytic *herbs* or *shrubs*; roots fibrous; stems succulent or woody, erect, terete. *Leaves* opposite, membranous to subcoriaceous, the stomata in groups on the lower surface. *Inflorescences* axillary; peduncles usually elongate, rarely lacking; bracts lacking. *Flowers* 1 to many per inflorescence; calyx lobes ovate to lanceolate, pubescent; corolla spurred, oblique in the calyx, either ventricose at the middle and the mouth constricted or narrowly campanulate with a broad, subregular to bilabiate limb, often spotted; stamens 4, included, the filaments adnate to the base of the corolla tube; disc annular and thickened posteriorly, reduced to the posterior glands, or semi-annular; ovary superior. *Fruit* a 2- or 4-valved fleshy capsule, laterally and apically compressed; seeds numerous.

Gasteranthus, a genus that includes about 25 species, was separated from *Besleria* L. by Wiehler (1975), who distinguished the two genera on the characters of fruit, leaves, and disc. *Gasteranthus* has a fleshy capsule (often difficult to discern from dried specimens) as opposed to a berry in *Besleria*, stomata arranged in groups on the lower leaf surface, and the variously shaped disc different from the annular disc found in the majority of *Besleria* species.

Species of *Gasteranthus* range from Guatemala to Peru in moist, shaded habitats.

The generic name alludes to the ventricose or bell-shaped flowers of some of the species.

Literature:

Morton, C. V. 1939. A revision of *Besleria*. Contr. U.S. Natl. Herb. 26(9): 395–474.

Wiehler, H. 1975. *Besleria* L. and the re-establishment of *Gasteranthus* Benth. (Gesneriaceae). Selbyana 1: 150–156.

a. Herbs with short stems; corolla broadly funnelform, more than 2 cm broad.
  b. Leaves subcoriaceous, not bullate, nearly glabrous; spur acuminate ..... 2. *G. delphinioides*
  bb. Leaves membranous, bullate, sericeous when young; spur blunt ..... 3. *G. dressleri*
aa. Shrubs often more than 1 m tall; corolla narrowly funnelform or scoop shaped, or if broader, then 1.5 cm wide or less.

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* See *Gasteranthus maculatus* Wiehl., Selbyana 5: 87, 1978.

c. Calyx lobes rotund; corolla ventricose; leaves often large, acute to obtuse ..... 4. *G. imbricans*

cc. Calyx lobes lanceolate or deltoid to ovate; corolla ventricose or not; leaves smaller, acuminate.

d. Corolla tube more than 1 cm broad at widest point, ventricose, spur elongate, obtuse ..... 1. *G. acropodus*

dd. Corolla tube less than 1 cm broad at widest point below limb, not ventricose, short spurred ..... 5. *G. wendlandianus*

1. **Gasteranthus acropodus** (J. D. Smith) Wiehl., Selbyana 1: 155. 1975.

Besleria acropoda J. D. Smith, Bot. Gaz. (Crawfordsville) 54: 240. 1912. TYPE: Forests of Tsaki, Talamanca, Prov. Limón, Costa Rica, *Tonduz 9554* (US, holotype).

B. allenii Morton, Ann. Missouri Bot. Gard. 29: 38. 1942. TYPE: Panamá, *Allen 2371* (US, holotype; MO, isotype).

B. allenii var. *paucivenia* Morton, Ann. Missouri Bot. Gard. 29: 38. 1942. TYPE: Panamá, *Allen 2188* (US, holotype; US, isotype).

Gasteranthus allenii (Morton) Wiehl., Selbyana 1: 155. 1975.

Terrestrial *subshrubs* or *shrubs*; stems erect, to 1(–5) m tall, the younger stems strigillose, the older stems glabrescent. *Leaves* subequal in a pair, more or less elliptic, 7–20 cm long, 3–7 cm wide, membranous, the apex acuminate, the base obtuse to attenuate and decurrent, serrulate or crenulate to remotely serrate, above dark green and glabrous, below pale green and sparsely strigillose; petiole 1–3 cm long, strigillose. *Inflorescences* axillary but appearing terminal by reduction of the main axis, umbellate or cymose, few flowered; peduncles 1.8–5.5 cm long, sparsely strigillose; pedicels 0.5–2.0 cm long, sparsely strigillose. *Flowers* with a broad receptacle, the calyx zygomorphic, the sepals distinct, unequal, serrate to nearly entire, whitish, pale green or purplish, the posterior lobe ovate or rhombic, keeled, 9–15 mm long, the 2 lateral lobes obliquely ovate, 8–15 mm long, the 2 anterior lobes lanceolate, slightly keeled, 6–15 mm long; corolla oblique in the calyx, mainly yellow, but varying from cream white to lemon yellow, with or without reddish lines, spots or patches, the tube ventricose and broad from a spurred base, 2.2–2.8 cm long, the spur 6–8 mm long, the tube to 1.5 cm broad at the middle, slightly narrowed just below the limb, sparsely pilose outside the limb, slightly bilabiate, ca. 1.5 cm broad, the lobes ca. 2–5 mm long; stamens 4, included, the staminode short, attached to the corolla base below the nectary, the filaments flattened, curved, the anthers 1–2 mm long, connate; disc thickened posteriorly, pubescent; ovary glabrous to sparsely pilose, style ca. 7 mm long, pubescent, stigma bilobed. *Fruit* oblate globose, ca. 5 mm long, 8 mm wide; seeds oblong, light brown, obliquely striate.

Gasteranthus allenii had been considered distinct from *G. acropodus* Wiehl because it lacked the spots on the corolla. However, from examination of recently collected material over the distributional range, it has become evident that corolla coloration is quite variable.

This species is known from both Costa Rica and Panamá, inhabiting moist forests mainly on the Caribbean slope.

BOCAS DEL TORO: Hill above RR station at Milla 7.5, *Croat & Porter 16378* (MO). Hillside above Almirante, *Gentry 2746* (MO). Quebrada Huron, *Kirkbride & Duke 432* (MO). Chiriquí Trail between Criollo, just above Buena Vista & Quebrada Higuerón, *Kirkbride &*

Duke 791 (MO). Water Valley, *Wedel 1420* (MO, US), *1475* (MO, US). Fish Creek Mountains, *Wedel 2272* (MO), *2346*, *2347* (both MO, US), *2351* (MO). Fish Creek Hills, *Wedel 2455* (MO, MO). COCLÉ: N rim, El Valle de Antón, 600 m, *Allen 1829* (MO, US). Hills N of El Valle de Antón, 1000 m, *Allen 2188* (US, US). La Mesa, N of El Valle de Antón, 1000 m, *Allen 2371* (MO, US). La Mesa above El Valle, 810 m, *Croat 25304* (MO). Hills N of El Valle de Antón, *Dressler 4388* (PMA). Cerro Gaital Caracoral, near Cerro Pilón, 2700–3200 ft, *Dwyer & Correa 8851* (MO, US). Mountains N of El Valle de Antón, 2500–3000 ft, *Lewis et al. 1755* (DUKE, MO, SCZ). COLÓN: Río Guanche 3–5 mi inland, 10–200 m, *Croat 26197* (MO), *26209* (PMA), 50–200 m, *Croat 36990* (MO); *Folsom 3767* (MO, US); *Foster et al. 2339* (DUKE); *Mori et al. 6441* (MO); *Mori & Kallunki 3012*, *3123* (both MO). Along old logging road above Río Iguanita, dense second growth forest, 390 m, *Skog et al. 4185* (US). PANAMÁ: Cerro Campana, *Croat 17231* (US); *Dressler 2984* (PMA), 3520 (PMA); *Kirkbride 240* (MO, NY); *Mori & Bolten 7684* (MO). SAN BLAS: SE of Puerto Obaldía, *Croat 16771* (MO).

2. **Gasteranthus delphinioides** (Seem.) Wiehl., Selbyana 1: 155. 1975.—FIG. 19.

Drymonia delphinioides Seem., Bot. Voy. Herald 186. 1854. TYPE: Cabo Corrientes, Chocó, Colombia, *Seemann 1054* (BM, holotype; photo, US).

Besleria subcoriacea Morton, Contr. U.S. Natl. Herb. 29(1): 28. 1944. TYPE: Bahia Solano, dense forest along Quebrada Jellita, Chocó, Colombia, *Killip & Garcia 33486* (US, holotype).

B. callista Standl. & L. O. Wms., Ceiba 1: 248. 1951. TYPE: Forested hills along the upper Río Piedras Blancas, vicinity of Río Esquinas, Prov. of Puntarenas, Costa Rica, *Allen 5589* (US, MO, isotypes).

B. delphinioides (Seem.) Leeuw., Acta Bot. Neerl. 8: 49. 1959.

Terrestrial *herbs* or low *shrubs*; stems erect with few branches, terete, pilose toward the apex, glabrescent below. *Leaves* nearly equal in a pair, lanceolate to ovate or elliptic, 7–16 cm long, 4.2–10.0 cm wide, subcoriaceous, the apex acute, the base cuneate, or acute, subentire to serrulate, above dark green, glabrous, below lighter green, with darker strigillose veins; petiole thick, 1.0–2.5 cm long, strigose. *Inflorescences* axillary but appearing terminal by reduction of the stem apex, shorter than the leaves; peduncles 2–7 cm long, sparsely pilose; pedicels ca. 1 cm long. *Flowers* showy, one to a few per inflorescence; calyx lobes nearly free, unequal, the anterior and the lateral lobes broadly ovate, to 1.5 cm long, ca. 1 cm wide at base, the posterior lobe deflexed by the corolla spur and longer, serrulate to entire, membranous to subcoriaceous, sparsely pilose; corolla white, yellow or pinkish, with reddish streaks or spots or orange yellow inside, horizontal in the calyx tube with a conspicuously curved acute spur ca. 2 cm long, campanulate, ventricose, 3.5–7.0 cm long, the limb bilabiate with the lower lobe exceeding the upper lobes, sparsely pilose, the lobes short and recurved; stamens held well within the corolla tube, ca. 1.5 cm long, the anthers coherent by their apices; stigma bilobed. *Fruit* and seeds not seen.

When in flower *Gasteranthus delphinioides* is distinctive by the large campanulate flowers which are almost certainly visited and pollinated by euglossine bees. In vegetative condition plants of this species resemble *G. acropodus*, but the latter species is usually larger in habit (1–5 m in height), found at higher elevations, and has membranous leaves.

Gasteranthus delphinioides ranges from Costa Rica to Colombia; in Panamá

FIGURE 19. *Gasteranthus delphinioides* (Seem.) Wiehl. Habit and flowers. (×½). [After *Foster 2810* (MO).]

plants may be found at low elevations in the provinces of Colón, Darién, Panamá, San Blas, and Veraguas.

COLÓN: Río Guanche ca. 3–5 mi inland, 10–100 m, *Croat 26176, 26209* (both MO). Río Guanche, *Foster 2810* (MO). DARIÉN: Ascent of Cerro Pirre from Río Pirre S of El Real, 750–1030 m, *Duke 5331* (MO). 10 mi S of El Real on Río Pirre, *Duke 5458* (MO). Quebrada Bidoto (Peccary Creek) off Río Aretí, *Duke 13600* (MO). Stream between Cerro Pirre and next southern peak, *Folsom 4371* (MO). Trail from Cerro Pirre to village of Pirre, *Gentry 4780* (MO). Manené to mouth of Río Cuasí, *Kirkbride & Bristan 1412* (MO). Río Balsa near Río Cuasí, *Kirkbride & Duke 1387* (MO). PANAMÁ: El Llano-Cartí highway 19 km N of El Llano, *Dressler 4277* (DUKE, F, MO, PMA). SAN BLAS: Trail to Darién from Puerto Obaldía, 10–15 km WSW of Puerto Obaldía, floodplain of Río Armila, *Mori et al. 6851* (MO). VERAGUAS: Guabal, Río Dos Bocas, 16 km NW of Santa Fé, 500 m, *Dressler 4815, 5022* (both PMA).

3. **Gasteranthus dressleri** Wiehl., Selbyana 2: 127. 1977. TYPE: About 1–2 km upstream on Río Guanche from bridge and road to Portobelo, Prov. Colón, Panamá, *Wiehler & Dressler 71165* (SEL, holotype, not available for study; US, isotype).

Terrestrial rosulate *herbs*; stems short, 2–7 cm long, pilose toward the apex, rooting from the lower nodes. *Leaves* flat on the ground, nearly equal in a pair,

broadly elliptic to obovate, 4.7–17.2 cm long, 3.0–9.7 cm wide, fleshy, the apex acute to obtuse or rounded, the base acute, occasionally oblique, dentate, above bullate, dark green and sparsely sericeous, below pale green, sericeous along the veins; petioles stout, 0.7–2.8 cm long, green, sericeous. *Inflorescences* axillary, reduced, cymose; peduncles 1–7 cm long, reddish, pilose, the pedicels ca. 3 cm long, reddish, sericeous. *Flowers* large and showy, 1–3 per inflorescence; calyx lobes free, lanceolate to elliptic, 1.3–1.7 cm long, ca. 7 mm wide, the apex acuminate, entire, green with the main veins reddish, the outside sericeous, the inside glabrous; corolla white with reddish lines along the veins and a yellow patch inside, horizontal in the calyx, funnel shaped, spurred at the base, the tube with curved blunt spur ca. 5 mm long, long pilose outside, inside glabrous, the limb broad, the lobes rotund, ca. 1.5 cm long and wide, entire; stamens included, filaments curved, ca. 1.5 mm long, glabrous, the anthers coherent by their apices, staminode present; disc a single bilobed posterior gland; style curved, ca. 1.5 cm long, the stigma stomatomorphic. *Capsule* surrounded by persistent calyx; seeds not seen.

Gasteranthus dressleri is known from the province of Colón in Panamá where it grows on damp clay banks. The plants superficially resemble the florists' Gloxinia (*Sinningia speciosa* cultivars) by its broad softly pubescent bullate leaves appressed close to the ground and by its broad corollas. The low appressed habit and pubescent bullate leaves distinguish this species from others in Panamá.

Duplicates at US of the paratypes reported from Colombia do not appear to be conspecific.

COLÓN: Hills just N of Río Guanche, 1–200 m, *Davidse & D'Arcy 10081* (MO, US). Río Guanche, ca. 2.5 km upriver from bridge on road to Portobelo, *Mori et al. 6466* (MO). Old logging road above Río Iguanita, 390 m, *Skog et al. 4180* (MO, US). 1–2 km upstream on Río Guanche from bridge and road to Portobelo, *Wiehler & Dressler 71165* (US).

4. **Gasteranthus imbricans** (J. D. Smith) Wiehl., Selbyana 1: 155. 1975.

Besleria imbricans J. D. Smith, Bot. Gaz. (Crawfordsville) 25: 155. 1898. TYPE: Forests of Shirores, Talamanca, Prov. Limón, Costa Rica, *Tonduz 9192* (US, holotype).
B. imbricans var. *uncinata* Morton, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1152. TYPE: Las Vueltas, Tucurrique, Prov. Cartago, Costa Rica, *Tonduz 13038* (US, holotype).
B. panamensis Morton, Contr. U.S. Natl. Herb. 26(9): 460. 1939. TYPE: Panamá, *Carleton 205* (US, holotype).
Gasteranthus panamensis (Morton) Wiehl., Selbyana 1: 155. 1975.

Terrestrial *subshrubs* or *shrubs*; stems erect, succulent when young, to 2 m tall, the apex minutely strigillose, soon becoming glabrous. *Leaves* subequal in a pair toward the apex of the branches, elliptic to broadly elliptic or ovate, 10–27 cm long, 5.3–16.7 cm wide, membranous, the apex acute, the base cuneate to obtuse, often oblique, subentire to irregularly serrate or dentate, above dark green, glabrous, below lighter green, strigillose along the veins; petioles 2–11 cm long, glabrate. *Inflorescences* in the upper axils, each several flowered, cymose or umbellate, irregularly compound; peduncles 7–17 cm long, glabrous; pedicels 0.8–1.8 cm long, glabrous. *Flowers* with the calyx zygomorphic, the lobes unequal, imbricate, distinct, broadly ovate, 0.7–1.2 mm long, membranous, entire to suberose, orange, glabrous, the anterior and the posterior lobes keeled;

corolla orange, horizontal in the calyx, spurred, the tube ventricose but contracted somewhat in the throat, 1.5–2.2 cm long, the outside glabrous, limb of 5 short nearly equal lobes, each ca. 2–3 mm long; stamens not exserted, the filaments flattened, ca. 1 cm long, glabrous, the anthers ca. 2.5 mm long, coherent by their apices; disc thickened posteriorly, pubescent; ovary subglobose, glabrous, the style ca. 8 mm long, glabrous, the stigma bilobed. *Capsule* broadly oblate, ca. 5 mm long, 8 mm wide, surrounded by the persistent calyx, orange; seeds oblong, light brown.

The broad calyx lobes and usually large leaves make this species distinctive. *Gasteranthus imbricans* and *G. panamensis* were originally described from collections of single specimens from nearby localities on either side of the Panamá-Costa Rica border. More recent collections and comparisons of the types have shown that they are the same taxon; differences are apparently due to maturity and exposure. In Panamá, *G. imbricans* has been found only in the province of Bocas del Toro at low elevations.

BOCAS DEL TORO: Sursuba, Río Changuinola, *Dwyer* 2899, *4387A*, *4900* (all MO). Quebrada Huron, 300–400 ft, *Kirkbride & Duke 450* (MO). Río Teribe near Quebrada Lukulon, 300 ft, *Kirkbride & Duke 508* (MO, MO, NY), *516* (MO). Duwebdulup Peak N of Río Teribe across from Quebrada Huron, 300–900 ft, *Kirkbride & Duke 573* (MO). Without other locality, *Carleton 205* (US).

5. **Gasteranthus wendlandianus** (Hanst.) Wiehl., Selbyana 1: 156. 1975.

Besleria wendlandianus Hanst., Linnaea 34: 318. 1865. LECTOTYPE: Turrialva, Prov. Cartago, Costa Rica, *Wendland 922* (B, probably not extant; photo, US).

Terrestrial or rarely epiphytic *shrubs*; stems to 2 m tall, when young succulent, lanate tomentose, woody and glabrescent with age. *Leaves* nearly equal in a pair, more or less elliptic, 8–20 cm long, 3–9 cm wide, membranous, the apex acuminate, the base acute, serrulate, above dark green, glabrous, below lighter green, tomentose on the veins, the secondary veins prominent; petioles 1–3 cm long, pubescent. *Inflorescences* in the upper leaf axils, cymose, few flowered; peduncles slender, arching upward, 4–7 cm long; pedicels 0.5–1.0 cm long. *Flowers* with the calyx nearly regular, the lobes distinct, deltoid, elongate, 6–9 mm long, longer in the fruit, the margins toothed, green, sparsely pilose; corolla yellow, red or purple spotted on the inside of the tube, slightly oblique in the calyx, the tube straight sided, basally saccate, 1.4–2.0 cm long, the outside pilose, the limb regular, terminal, ca. 1 cm wide, the lobes 2–3 mm long; stamens 4, staminode lacking, the anthers connate, ca. 1 mm wide; disc thickened posteriorly; ovary pubescent, the style ca. 6 mm long, pubescent, the stigma bilobed. *Capsule* globose, 6–7 mm long and wide, surrounded by the persistent calyx, yellow; seeds ellipsoid, tawny.

This species is found in Costa Rica and in the provinces of Bocas del Toro, Chiriquí, Darién, and Veraguas in Panamá, mainly growing in damp, heavily shaded forest.

BOCAS DEL TORO: Róbalo Trail N slopes of Cerro Horqueta, 6000–7000 ft, *Allen 4920* (MO). Chiriquí trail between Buena Vista coffee finca and Cerro Pilón, *Kirkbride & Duke*

706 (MO, NY, REED). Without other locality, *Wedel 300* (NY). CHIRIQUÍ: NW side of Cerro Pando, *Croat 15957* (MO). Cerro Colorado on upper mining road 20 to 28 mi from San Félix, 1200–1500 m, *Croat 33293* (MO, US). Bajo Chorro, Boquete District, 6000 ft, *Davidson 381* (F). Camp Hornitos, Fortuna dam site, 1200 m, *Dressler 5354* (PMA). Between Pinola and Quebrada Hondo toward summit on Chiriquí trail, *Kirkbride & Duke 886* (MO, REED). Road at Quebrada El Velo near Finca Lérida, 6 km NW of Boquete, 1700 m, *Nee 10618* (MO). Bajo Mono at Río Chiquero, 1800 m, *Skog et al. 4060* (MO, US). Bajo Chorro, 1900 m, *Woodson & Schery 669* (MO, US). DARIÉN: Cerro Pirre, 2500–4500 ft, *Duke & Elias 13683* (MO, REED). Between Cerro Pirre and next southern peak, *Folsom 4367* (MO, US). VERAGUAS: 0.6 mi beyond Escuela Agricola Alto Piedra, 730 m, *Croat & Folsom 34022, 34023* (both MO). Third branch of Río Santa María 12 km NW of Santa Fé, 650 m, *Dressler 5006* (PMA). Ridge road at Cerro Colorado, 7.6 km from main road along stream, 1450–1750 m, *Folsom et al. 4822* (US).

13. GLOXINIA

Gloxinia L'Hér. in Aiton, Hort. Kew. 2: 331. 1789, non *Gloxinia* Regel. TYPE: *G. maculata* L'Hér., illegitimate name for *Martynia perennis* L. = *Gloxinia perennis* (L.) Fritsch.

Eucolum R. A. Salisb., Prodr. Stirp. 98. 1796. TYPE: *E. crassifolium* R. A. Salisb., illegitimate name for *Martynia perennis* L. = *Gloxinia perennis* (L.) Fritsch.

Mandirola Decne., Rev. Hort. 20 [sér. 3, 2]: 468. 1848. TYPE: *M. multiflora* (G. Gardner) Decne. = *Gloxinia hirsuta* (DC.) Wiehl.

Salisia Regel, Flora 32: 179. 1849, illegitimate substitute name for *Gloxinia* L'Hér. TYPE: *S. gloxiniaeflora* Regel, illegitimate name for *Martynia perennis* L. = *Gloxinia perennis* (L.) Fritsch.

Seemannia Regel, Gartenflora 4: 183. 1855. TYPE: *S. ternifolia* Regel = *Gloxinia sylvatica* (Kunth) Wiehl.

Achimenes subg. *Mandirola* (Decne.) Hanst., Linnaea 34: 434. 1865.

A. sect. *Mandirola* (Decne.) Benth. in Benth. & Hook. f., Gen. Pl. 2: 999. 1876.

A. sect. *Kohleriopsis* Fritsch in Engler & Prantl, Nat. Pflanzenfam., Nachtr. 1: 300. 1897. TYPE: *A. heppielloides* Fritsch = *Gloxinia gymnostoma* Grisebach.

Fritschiantha Kuntze, Rev. Gen. 3(2): 241. 1898. Based on *Seemannia* Regel = *Gloxinia* L'Hér.

Achimenes sect. *Tydaeopsis* Fritsch, Bot. Jahrb. Syst. 50: 395. 1913. TYPE: *Achimenes rusbyi* N. L. Britton = *Gloxinia gymnostoma* Grisebach.

Fiebrigia Fritsch, Bot. Jahrb. Syst. 50: 397. 1913. TYPE: *F. digitaliflora* Fritsch = *Gloxinia gymnostoma* Grisebach.

Perennial *herbs* from scaly rhizomes; stems usually erect. *Leaves* opposite, nearly equal in a pair, the base not oblique, entire or toothed; petiolate. *Inflorescences* of single flowers in the axils of the leaves or arranged opposite in a pair on racemes in the axils of reduced leaves. *Flowers* showy; floral tube often elongate, narrow, grooved; calyx 5-lobed; corolla white, blue, lavender, rose pink, tubular, funnelform to campanulate, erect or oblique in the calyx, the limb of 5 nearly equal lobes; fertile stamens 4, the filaments often coiling after anthesis, the anthers coherent by their apices; disc absent or annular when present; ovary inferior. *Fruit* an elongated capsule; seeds numerous.

Gloxinia is a genus of about 10 species distributed in South America in Bolivia, Brazil, Columbia, Peru, and Venezuela. Some species are in cultivation as ornamentals and occasionally escape from cultivation in tropical regions. The type species, *G. perennis*, may be wild in Panamá but its rarity and its occurrence near areas of habitation or which have been under settlement for long periods of time suggest that the species may, in fact, be naturalized.

The genus may be distinguished most easily from the closely related *Monopyle* by the oblique leaves in the latter genus.

The commonly cultivated plants known as "Florists-Gloxinia" are actually cultivars of *Sinningia speciosa* (Lodd. ex Ker-Gawl.) Hiern.

Gloxinia is named for Benjamin Peter Gloxin, an Alsatian botanist and physician of Colmar of the late 18th Century.

Literature:

Hoehne, F. C. 1964. O gênero *Gloxinia* no Brasil. Arq. Bot. Estado São Paulo 3(6): 315–335.

Vogel, S. 1966. Parfümsammelnde Bienen als Bestäuber von Orchideen und *Gloxinia*. Oesterr. Bot. Z. 113(3–4): 302–361.

1. **Gloxinia perennis** (L.) Fritsch in Engler & Prantl, Nat. Pflanzenfam. 4(3b): 174. 1894.—FIG. 20.

Martynia perennis L., Sp. Pl. 618. 1753. TYPE: Hort. Cliff. 322, *tab. 18*. 1738, Cult. Hort. Cliffortianus (BM, not seen).

Gloxinia maculata L'Hér. in Aiton, Hort. Kew. 2: 331. 1789, illegitimate name for *Martynia perennis* L. = *Gloxinia perennis* (L.) Fritsch.

Eucolum crassifolium R. A. Salisb., Prodr. Stirp. 98. 1796, illegitimate name for *Martynia perennis* L. = *Gloxinia perennis* (L.) Fritsch.

Gloxinia trichotoma Moench, Suppl. 194. 1802, illegitimate name for *Martynia perennis* L. = *Gloxinia perennis* (L.) Fritsch.

G. heterophylla Poepp. in Poepp. & Endl., Nov. Gen. 3: 9. 1840. TYPE: Pampayaco, Peru, *Poeppig* (not seen).

G. pallidiflora Hook., Bot. Mag. 72: *tab. 4213*. 1846. TYPE: Santa Marta, Colombia, *Purdie* (K, not seen).

G. suaveolens Decne., Rev. Hort. 20 [sér. 3, 2]: 463. 1848. TYPE: not seen.

Salisia gloxiniaeflora Regel, Flora 32: 179. 1849, illegitimate name for *Martynia perennis* L. = *Gloxinia perennis* (L.) Fritsch.

Gloxinia trichantha Miq., Linnaea 22: 473. 1849. TYPE: Cult., Surinam, *Focke* (not seen).

Salisia maculata (L'Hér.) Regel, Bot. Zeitung (Berlin) 9: 894. 1851.

S. *pallidiflora* (Hook.) Regel, Bot. Zeitung (Berlin) 9: 894. 1851.

S. *suaveolens* (Decne.) Regel, Bot. Zeitung (Berlin) 9: 894. 1851.

Herbs from rhizomes with auricular scales; stems herbaceous to 1 m tall, smooth and nearly glabrous, green, streaked or spotted with red or suffused with red toward the bases of the internodes, unbranched or with few branches. *Leaves* nearly equal in a pair, ovate, 5.5–12.7 cm long, 3.4–8.9 cm wide, the apex acute, the base acute, truncate to cordate, coarsely crenate, above dark green, glossy, glabrous to sparsely strigose, below white, or light green, often suffused with red purple; petioles 1.4–4.7 cm long, 1–2 mm wide, green or reddish, sparsely pilose. *Inflorescences* terminal elongate racemes; peduncles similar to the stem internodes, green or streaked with red, to 12.5 cm long; bracts leaflike, but reduced; pedicels opposite, to 1.5 cm long. *Flowers* solitary in the axils of the bracts, showy; floral tube elongate, narrow, 0.5–1.0 cm long, enlarging in fruit, with 10 longitudinal grooves, green or red spotted, glandular; calyx lobes subequal, spreading, lanceolate to oblong, 0.7–1.0 cm long, 4–7 mm wide, light green, sometimes streaked with red outside, glabrous, inside darker green, the apex entire to serrate; corolla white, lavender to purple, oblique in the calyx,

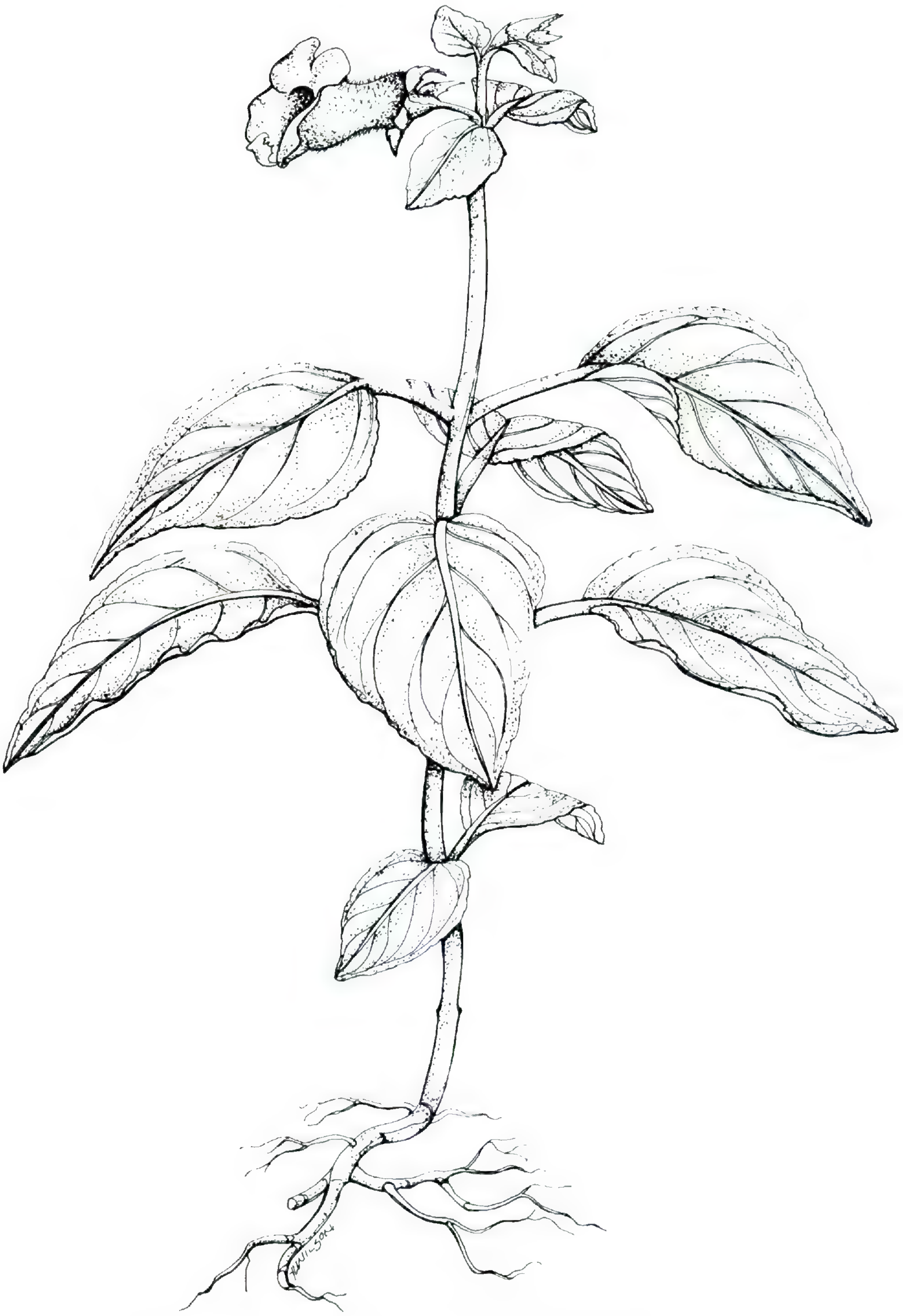

FIGURE 20. *Gloxinia perennis* (L.) Fritsch. Habit (×7/10). [After *Allen 2280* (MO).]

campanulate with a broad gibbous base, ca. 1 cm wide, ca. 1.8 cm wide near the limb, the tube 1.5–2.0 cm long, pilose outside, the inside glandular on the upper surface with a dark violet patch in the basal pouch, the limb lobes nearly equal in size, the upper and the lateral lobes spreading and entire, the basal lobe incurved with a toothed margin; filaments straight at anthesis, densely pilose and glandular, coiling after the pollen has been released, the anthers triangular, coherent by the apices; the disc annular and short when present, often apparently lacking; ovary apex pubescent, the style glandular, pilose, the stigma stomatomorphic. *Capsule* narrowly conic. *Chromosomes* $2n = 26$ (Rogers, 1954).

Gloxinia perennis was brought into cultivation from Colombia in 1739 to the Chelsea Physic Garden, thus, one of the earliest of the gesneriads to be cultivated in Europe. It is now widely cultivated as a pot plant in temperate regions and outdoors in warmer areas.

The shape of the flowers of *Gloxinia perennis* is similar to those of some species of *Campanula*, and the plants are commonly known as the Canterbury-Bells Gloxinia.

In addition to Colombia, the species is known from Peru and Venezuela. In Panamá plants have been collected in the Canal Zone and in the province of Panamá.

Vogel (1966) discussed the association of *Gloxinia perennis* with euglossine bees and the function of the dark violet spot at the base of the corolla which apparently provides perfume for the bee's mating ritual.

CANAL ZONE: Government Forest Preserve, Madden Road, 50 m, *Allen 2280* (MO, US). Planted, Mount Hope Cemetery, *Standley 28842* (US). PANAMÁ: Mocambo S of Las Cumbres, open area beside road, *Croat 12529* (MO).

14. KOELLIKERIA

Koellikeria Regel, Ind. Sem. Hort. Bot. Turic. [4]. 1847. TYPE: *K. argyrostigma* (Hook.) Regel = *K. erinoides* (DC.) Mansfeld.

Terrestrial *herbs* from scaly rhizomes; stems often reduced, unbranched, pilose. *Leaves* often congested into a rosette, opposite, equal in a pair; blades soft, pubescent, crenate to serrate; petioles usually short. *Inflorescences* terminal, elongate racemes; peduncles elongate; bracts alternate, minute, bearing in their axils the short pedicels. *Flowers* numerous, the floral tube turbinate, pilose; calyx lobes 5, free, equalling the length of the floral tube; corolla tubular, nearly erect in the calyx, and not spurred, 5-lobed, 2-lipped, the upper 2 lobes short and exceeded by the much longer and toothed 3 lower lobes; stamens 4, adnate to base of the corolla tube, the anthers united by their sides and apices; disc a nectariferous ring; ovary ½ inferior, the stigma bilobed. *Fruit* a capsule.

Koellikeria is a genus of 2–3 species that occurs from Costa Rica south to Venezuela, Bolivia and Argentina. The species which occurs in Panamá also occurs throughout the range of the genus. *Koellikeria erinoides* has been in cultivation for many years as a house plant or greenhouse specimen because of its low habit and relative ease of culture.

From other rhizomatous gesneriads, *Koellikeria* can be distinguished by the rosette habit, the racemose inflorescence with alternate arrangement of flowers, and the strongly bilabiate corolla. The leaves appear as if speckled with silver dots.

Koellikeria is named for Rudolf Albrecht von Kölliker, 1817–1905, Swiss, a teacher of microscopic and human anatomy, but as a botanist he compiled a flora of the canton of Zurich in 1839.

Literature:

Batcheller, F. N. 1970. Gesneriads one by one: *Koellikeria*. The Gloxinian 20(4): 9–11, 31.

1. **Koellikeria erinoides** (DC.) Mansfeld, Repert. Spec. Nov. Regni Veg. 38: 28. 1935.—FIG. 21.

Achimenes erinoides DC., Prodr. 7: 536. 1839. TYPE: Caracas, Venezuela, Vargas (G-DC, holotype; US, photo).
A. argyrostigma Hook., Bot. Mag. 71: *tab. 4175*. 1845. TYPE: Sierra Nevada de Sta. Marta, Colombia, *Purdie* (K, holotype, not seen).
Koellikeria argyrostigma (Hook.) Regel, Ind. Sem. Hort. Bot. Turic. [4]. 1847.
K. argyrostigma var. *ovalifolia* Oerst. Cent., Gesn. 15. 1858. TYPE: San Lucas Island, Costa Rica, *Oersted* (C, type; US, photo).

Terrestrial *herbs*; stem erect or decumbent, short, the internodes reduced or rarely elongated to 15 cm, green or reddish, tomentose or pilose. *Leaves* often clustered at the apex of the stem in a flat rosette, elliptic to obovate, 1.5–11.3 cm long, 1.3–4.9 cm wide, membranous, the apex acute to obtuse, the base acute or broadly cuneate, crenate, dark green above, sometimes reddish along the immersed veins, randomly maculate with silvery spots, pilose, the lower surface light green or with a reddish margin or suffused with purple throughout, pilose, the veins prominent. *Inflorescences* terminal or in the axils of the upper leaves, of many flowers in a raceme, erect, to 30 cm tall but usually shorter, green to purple, pilose; peduncles to ½ the length of the inflorescence; bracts lanceolate, 1–2 mm long, ca. 1 mm wide; pedicels alternate, ca. 1 cm long or less. *Flowers* small, the floral tube turbinate, 1–2 cm long and wide, green to reddish, pilose; calyx lobes erect, linear to lanceolate, 1–2 mm long, the apices somewhat spreading, all green, with reddish lines, or with apices reddish, pilose; corolla bilabiate, erect to somewhat oblique in the calyx, the tube broadened transversely, gibbous at the base on upper side, ventricose at the middle, short, ca. 5 mm long, 3 mm broad, sparsely pilose, all white, creamy, or red on upper side and white on the lower, inside yellowish with red or orange lines on the lower side, the upper 2 lobes erect, 1–2 mm long and wide, usually reddish, the margin white, subentire, the lower lobes 2–3 times as long as the upper lobes, erect to porrect, white, the margin erose to fimbriate, curved upwardly; stamens 4 with a reduced staminode, equalling the length of the corolla tube, the filaments curved, adnate to the corolla at the base, white, glandular at the base, glabrous above, the anthers white, coherent, ca. 1 mm long, pubescent on the back; disc a yellowish ring; ovary ½ inferior, the apex pilose; style curved, white, glabrous, the stigma

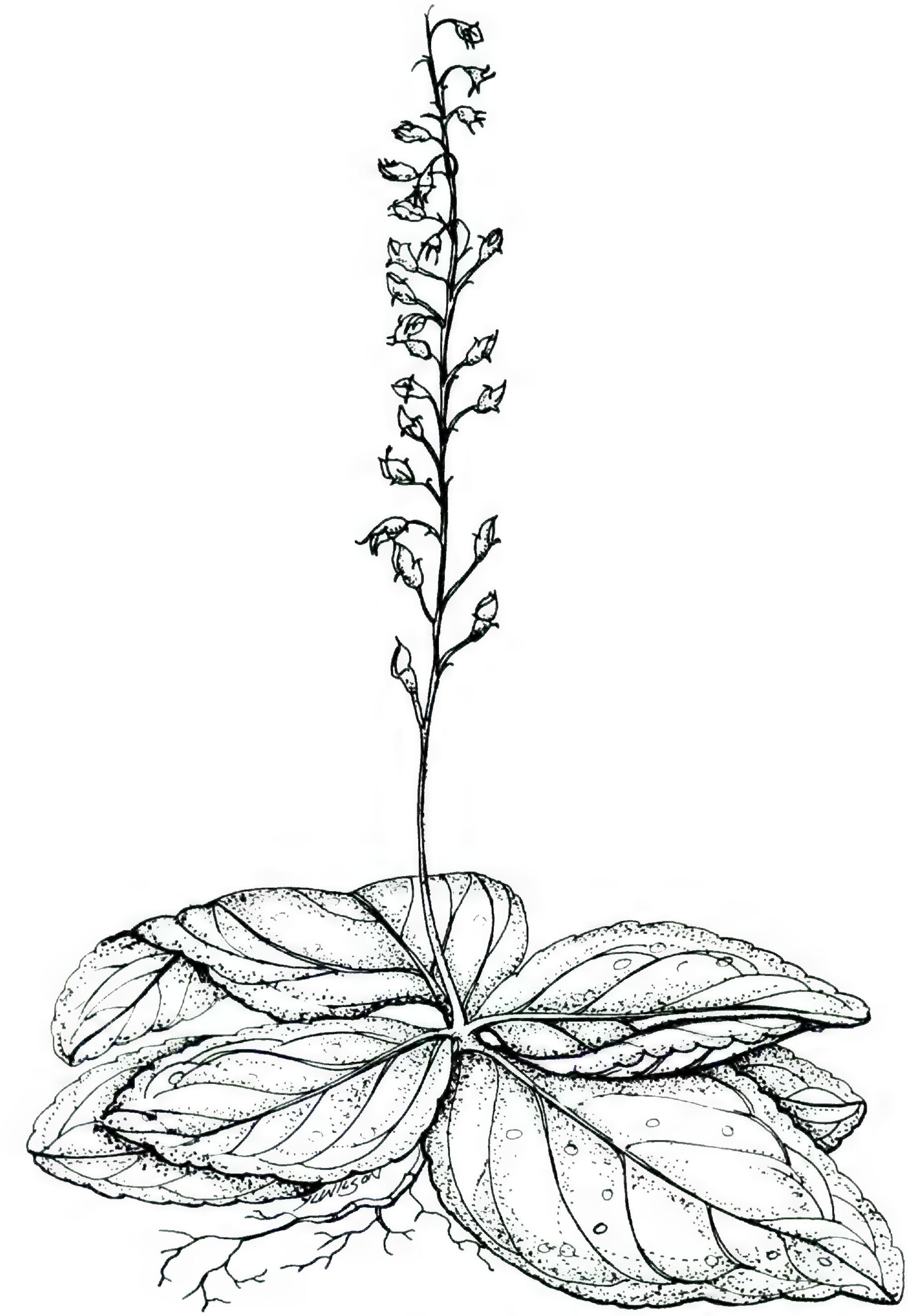

FIGURE 21. *Koellikeria erinoides* (DC.) Mansf. Habit (×1). [After *Blum & Tyson 637* (MO).]

shortly bilobed. *Capsule* ellipsoid, ca. 5 mm long, brown; seeds ellipsoid, striate, ca. 0.5 mm long. *Chromosomes* $n = 13$ (Fussell, 1958 from material collected in Venezuela).

The silvery spots on the leaves are distinctive and make this species readily recognizable.

Koellikeria erinoides occurs in colonies on rocks or banks near streams, or in damp shaded areas. The plants are dormant during early winter, reduced to the underground rhizomes. In Panamá the species occurs in the provinces of Chiriquí, Coclé, and Veraguas. It may be expected elsewhere since it is wide-ranging from Costa Rica to Bolivia and Venezuela.

CHIRIQUÍ: Trail from San Félix to Cerro Flor, 100–850 m, *Allen 1922* (MO, NY, US). 5 mi S of Boquete, 3000 ft, *Allen 4697* (MO, US). Hamlet of Cerro Otoe, 15–20 km N of San Félix, 3000 ft, *Bort 71* (MO). Cerro Colorado, near mining camp, 750–800 m, *Dressler 5131* (MO, PMA). Llano Francia, 4 mi from Boquete toward Dolega, 4500 ft, *Dwyer & Hayden 7601* (MO). Tolé, Santa Ana Well, 1000 ft, *Dwyer & Kirkbride 7445* (MO). Cerro Colorado, area surrounding stream by Escopeta, *Folsom 4903* (MO, US). From Boquete to 3 mi N, 3300–4200 ft, *Lewis et al. 352* (MO). 5 mi S of Boquete toward David, 2800 ft, *McDaniel 6804* (MO). Tolé, *Tyson et al. 4227* (FSU, MO, SCZ). Boquete, 1200–1500 m, *Woodson & Schery 761* (MO, US). COCLÉ: Picacho de Olá, 350–600 m, *Pittier 5060* (US). VERAGUAS: 5 mi NE of La Mesa, *Blum & Tyson 637* (FSU, MO, SCZ). Santiago, 4 mi from Panamerican Highway toward Atalaya, *Dwyer & Kirkbride 7423* (MO). Stream which feeds Laguna La Yeguada, 15 km N of Calobré, 644 m, *Luteyn 1454* (DUKE).

15. KOHLERIA

Kohleria Regel, Ind. Sem. Hort. Bot. Turic. [4]. 1847. TYPE: *K. hirsuta* (Kunth) Regel.

Isoloma Benth. ex Decne., Rev. Hort. 20 [sér. 3, 2]: 465. December, 1848, not *Isoloma* J. Smith, 1841. TYPE: *I. hirsutum* (Kunth) Regel = *Kohleria hirsuta* (Kunth) Regel.

Tydaea Decne., Rev. Hort. 20 [sér. 3, 2]: 468. December, 1848. TYPE: *T. picta* (Benth. ex Hook. f.) Decne. = *Kohleria bogotensis* (Nichols.) Fritsch.

Giesleria Regel, Flora 32: 181. 1849. TYPE: *Achimenes picta* Benth. ex Hook. f. = *Kohleria bogotensis* (Nichols.) Fritsch.

Sciadocalyx Regel, Gartenflora 2: 257. 1853. TYPE: *S. warszewiczii* Regel = *Kohleria warszewiczii* (Regel) Hanst.

Brachyloma Hanst., Linnaea 26: 203. 1854, not *Brachyloma* Sonder, 1845. TYPE: *B. hirsutum* (Kunth) Hanst. = *Kohleria hirsuta* (Kunth) Regel.

Calycostemma Hanst., Linnaea 29: 506. 1859. TYPE: *C. lindenii* Hanst. = *Kohleria lindenii* (Hanst.) Hanst.

Cryptoloma Hanst., Linnaea 29: 506. 1859. LECTOTYPE: *C. hondensis* (Kunth) Regel = *Kohleria hondensis* (Kunth) Regel.

Terrestrial *herbs*, *subshrubs*, or *shrubs* from scaly rhizomes; stems usually erect or decumbent, terete, green to reddish brown, hirsute with multicellular hairs. *Leaves* opposite or in whorls of 3–4, those of a pair nearly equal to unequal, pilose or hirsute, the blades thickened, ovate, lanceolate, or elliptic, serrate or crenate, dark green above, light green to purplish below, the lateral veins 6–9 arching toward the apex; petioles short or long. *Inflorescences* with flowers solitary, fasciculate to umbellate, usually numerous in the upper leaf axils, often appearing racemose or spicate with reduced leaves; peduncles often short with long pedicels, green or reddish, hirsute. *Flowers* protandrous, somewhat zygo-

morphic, 1–4 per peduncle; floral tube turbinate to globose, hirsute; calyx lobes thick, erect to recurved, equalling or longer than the floral tube, pubescent on both the surfaces; corolla of 5 petals connate into a tube, erect or oblique in the calyx, the limb 5-lobed, bilabiate or regular, usually spotted or striped, the tube usually ventricose at the middle or toward the throat, or campanulate above a narrow base, red hirsute outside, sparsely pubescent inside; fertile stamens 4, adnate to the base of the corolla tube, the anthers at first coherent, later often becoming free, thecae distinct, dehiscent by longitudinal slits, a staminode usually present; disc lobate or of 5 glands, free or with 2 united; ovary more than ½ inferior, the style pubescent, the stigma bilobed, the ovules numerous on both the surfaces of the placental lamellae. *Fruit* a dry capsule dehiscing into 2 valves, the apex conic or rostrate; seeds numerous, fusiform, striate, dark brown.

Kohleria is a genus with many species that ranges from México to South America. The genus is widely cultivated for its colorful flowers. Numerous hybrids and cultivars are available in the horticultural trade.

Three species are known from Panamá, *Kohleria spicata*, *K. tubiflora*, and *K. allenii*. The first two are common, but the third is rare in Panamá.

Literature:

Moore, H. E. 1953. Comments on some Kohlerias cultivated in the United States. Baileya 1: 89–101.

Morton, C. V. 1967. The Genus *Kohleria* in Mexico [Gesneriaceae]. Baileya 15: 61–78.

———. 1967. A new *Kohleria* from Costa Rica in cultivation [Gesneriaceae]. Baileya 15: 79–81.

Williams, L. O. 1968. A beautiful Costa Rican *Kohleria*. Notes Roy. Bot. Gard. Edinburgh 28(3): 291–292.

a. Cauline leaves 3 to 4 at a node; corolla limb diameter broader than the widest part of the tube, lobes spreading or reflexed.
   b. Corolla yellow with red hairs on outside, tube campanulate, 2.5–3.0 cm long, ca. 1.5 cm wide, all lobes equally spreading ..... 1. *K. allenii*
   bb. Corolla deep red to orange red outside, tube cylindric, not campanulate, 1.2–2.0 cm long, ca. 1 cm wide, upper and lateral lobes spreading, basal lobe reflexed ..... 2. *K. spicata*

aa. Cauline leaves 2 at a node; corolla limb diameter less than widest part of the tube, lobes erect ..... 3. *K. tubiflora*

1. **Kohleria allenii** Standl. & L. O. Wms., Notes Roy. Bot. Gard. Edinburgh 28: 291. 1968. TYPE: Prov. Puntarenas, Costa Rica, *Allen 6300* (F, holotype; US, isotype).

Woody *herbs*; stem round or angled, erect or ascending, 1.0–1.5 m tall, reddish above, brownish below, pilose. *Leaves* 2–4 at a node, reduced above. lanceolate to ovate, 5–8 cm long, 2.5–4.0 cm wide, acute to acuminate, serrulate, reddish, the base acute to subtruncate, above dark green, sparsely pilose to scabrous, below light green, densely pilose; petioles 0.5–2.0 cm long. *Inflores-*

cences few flowered in the axils of the upper reduced leaves; peduncles not evident; bracts ovate, ca. 5 mm long, green, pilose; pedicels elongate, ca. 4 cm long, green or reddish, pilose. *Flowers* showy, the floral tube oblique, gibbous to 1 side, rounded, green or reddish, pilose; calyx 5-lobed, the lobes connate briefly at the base, triangular ovate, 5–8 mm long, accrescent in fruit, green with red margins, pilose; corolla cylindric campanulate, 25–30 mm long, ca. 5 mm wide at base, broadening to 1.5 cm broad at middle and above, yellow with red hairs outside, inside red maculate, glandular; stamens 4, equalling the corolla, the anthers coherent in 2 pairs; disc sublobate; ovary apex pilose, the style ca. 2 cm long, the stigma bilobate. *Fruit* many seeded enclosed in the persistent calyx; seeds fusiform, acuminate at both ends, ca. 0.25 mm long, striate.

Kohleria allenii is rare in Panamá, found only in the province of Chiriquí, but is somewhat more common in Costa Rica. Its habitat is dry, steep hillsides at ca. 500 m elevation.

This species in floral characters is reminiscent of *Capanea grandiflora* with its large campanulate spotted corolla.

CHIRIQUÍ: San Bartolo Limite, 19 km W of Puerto Armelles, 500 m, *Busey 609* (MO, NY).

2. **Kohleria spicata** (Kunth) Oerst.,[15] Cent. Gesn. 27. 1858.—FIG. 22.

Gesneria spicata Kunth, in H.B.K., Nov. Gen. Sp. 2: qto. ed. 393; fol. ed. 316. 1818. TYPE: Quindio, Colombia, *Bonpland 1815* (P, not seen; US, photo).
G. petiolaris Benth., Bot. Voy. Sulphur 131. 1845. TYPE: "Island off the coast of Veragua," Panamá, *Barclay* (BM, not seen).
G. seemannii Hook., Bot. Mag. 76: *tab. 4504.* 1850. TYPE: Darién, Panamá, *Seemann* (K, not seen).
Isoloma petiolare (Benth.) Regel, Bot. Zeitung (Berlin) 9: 893. 1851.
Kohleria seemannii (Hook.) Hanst., Linnaea 26: 203. 1854.
Brachyloma petiolare (Benth.) Oerst., Cent. Gesn. 30. 1858.
Kohleria incana Klotzsch & Hanst., Linnaea 29: 522. 1859. TYPE: "Costa Rica et Veragua," *Warszewicz 29* (B, not seen).
Isoloma seemannii (Hook.) Benth., in Benth. & Hook. f., Gen. Pl. 2: 1002. 1876.
I. incanum (Klotzsch & Hanst.) Hemsl. in Godm. & Salv. Biol. Cent. Amer., Bot. 2: 478. 1882.
Kohleria longifolia (Lindl.) Hanst. var. *petiolaris* (Benth.) Morton, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1180. 1938.

Terrestrial coarse *herbs* or rarely suffruticose; rhizomes scaly, pink, pubescent; stems simple, erect, stout, terete, to 1.5 m tall, to 7 mm in diam., green to usually reddish, villous hirsute with spreading red or brown many-celled hairs, unbranched or branched only from the base. *Leaves* opposite or ternate, those at a node usually similar in size, petiolate, membranous, narrowly elliptic to lanceolate, 7–15(–28) cm long, 2.9–5.5 cm wide, the base cuneate to obtuse, crenate serrate, sometimes minutely so, rarely reddish, the apex acute to acuminate, the upper surface dark green, hirsute, becoming scabrous with age, the lower surface lighter green, rarely reddish, tomentose, lateral veins 5–9; petioles sulcate, 1.3–2.5(–4.5) cm long, reddish, villous. *Inflorescences* in fascicles of 1–5 flowers in axils of the leaves, the leaves reduced above on short

[15] Only those names used for Panamá plants have been included.

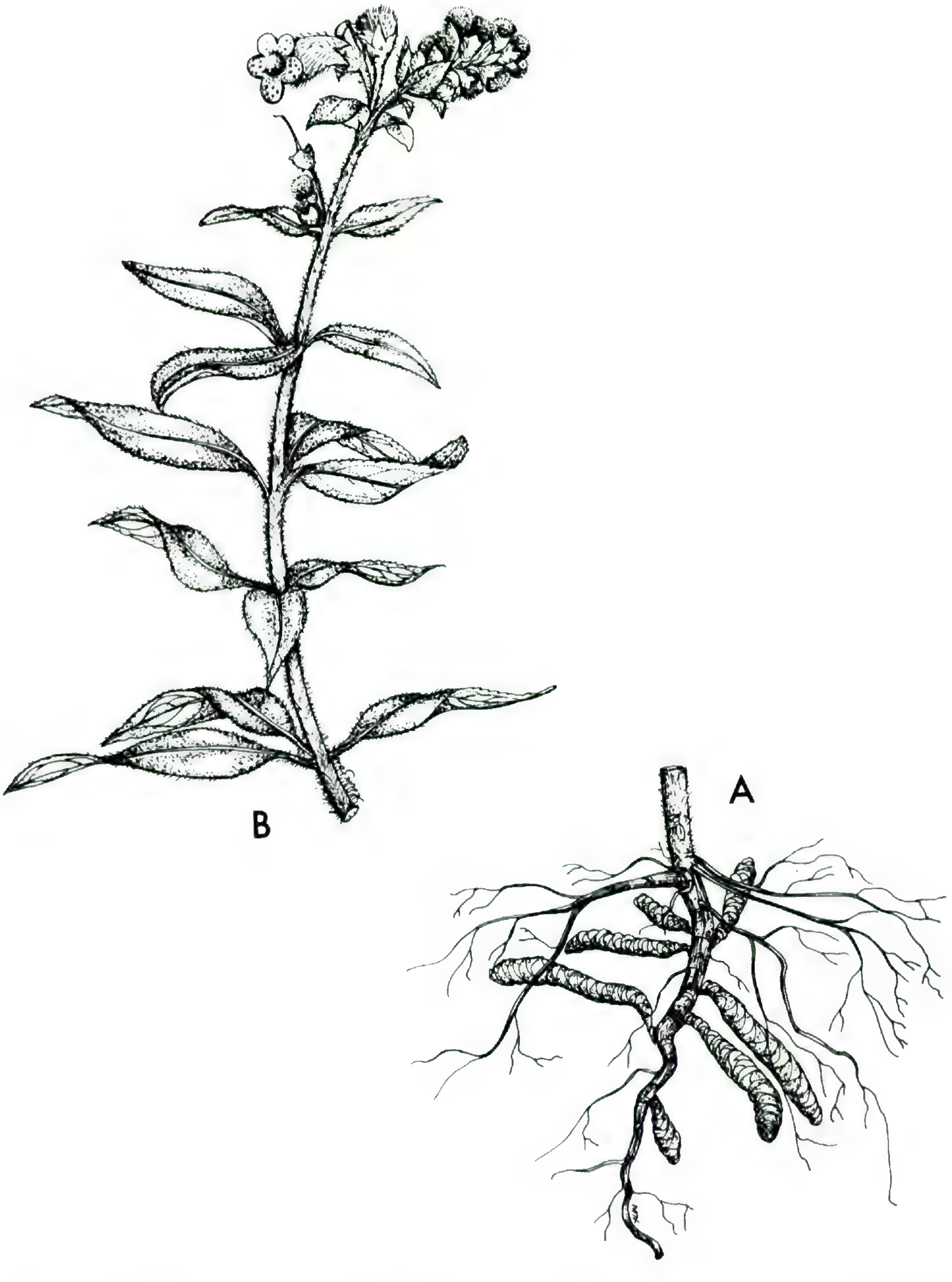

FIGURE 22. *Kohleria spicata* (Kunth) Oerst.—A. Base of plant with rhizomes (×⅗). [After *Busey 450* (MO).]—B. Habit (×⅗). [After *Stern et al. 1210* (US).]

internodes giving the appearance of a raceme 5–35 cm long; peduncles lacking; pedicels to 2.5 cm long, reddish or brown, hirsute. *Flowers* with floral tube turbinate, 2–3 cm long, densely hirsute; calyx lobes erect, equal, thick triangular ovate to oblong, 2–5 mm long, green, red or brown, hirsute on both sides, the

apex acute or obtuse; corolla deep red to orange red outside, the inside paler with red spots, red villous outside, the inside glandular, tubular, 1.2–1.8(–2.0) cm long, 4–5 mm wide at the slightly oblique base, ampliate or ventricose, 5–7 mm wide at the middle, then slightly contracted at the throat, the mouth oblique, the limb bilabiate of 5 lobes to 1 cm across, the lateral and the upper lobes spreading, the basal lobe reflexed, all nearly equal, obtuse or rounded, 2–4 mm long and wide, glabrous to pilose glandular, entire; stamens 4, not exserted, the filaments broad at the base and adnate to the base of the corolla tube, narrowed above, yellow, glabrous, the anthers oblong, ca. 2 mm long, pilose on back, staminode much reduced; glands 5, usually free or the 2 posterior glands more or less united; ovary apex conic, hirsute, the style curved, ca. 1 cm long, glandular pilose, the stigma bilobed. *Fruit* a globose capsule surrounded by the persistent floral tube, 5–7 mm in diam., red to brown, villous; seeds numerous, fusiform, ca. 0.5 mm long, reddish brown. *Chromosomes* $2n = 26$ (Rogers, 1954).

Kohleria spicata is the most widespread of all species of *Kohleria* and is found from southern México to northern South America. Plants are commonly encountered in Panamá on damp weedy roadside banks, often in full sun. The plants become dormant during dry periods, then resprout from rhizomes when conditions are more favorable.

Populations are quite variable, apparently depending upon soil conditions and exposure.

BOCAS DEL TORO: Changuinola River near Old Ford, *Dunlap 173* (F, US). CHIRIQUÍ: Burica Peninsula, Rabo de Puerco, 8 km W from Puerto Armuelles, 150 m, *Busey 450* (MO). Cafetales just above El Cantinero (Boquete), *D'Arcy 9820, 9825* (both MO). E side of Cerro Pando (near Río Chiriquí Viejo), 6000 ft, *D'Arcy & D'Arcy 6612* (US). 30 km W of Volcán, road to Río Sereno, *Dressler 4899* (PMA). Lava fields near the town of Volcán, 4600 ft, *Duke 9167* (MO). Between Boquete and Cerro Horqueta, *Duke A13717* (MO, SCZ). 7 mi S of Volcán on road from David, 600–750 m, *Graham 254* (MICH). From Boquete to 3 mi N, 3300–4200 ft, *Lewis et al. 337, 609* (both MO, SCZ). Edge of steep river bank 12.4 mi N of David, *Lewis et al. 715* (MO, SCZ). Road 3–5 mi NW of El Hato del Volcán towards Costa Rica across the Río Chiriquí Viejo, 3000–4000 ft, *Luteyn 857* (DUKE). Road to Volcán 15 km N of Concepción, *Skog et al. 4013* (E, MO, P, PMA, US). Tributary of Río Caldera ca. 4 km NW of Boquete, 1400 m, *Skog et al. 4063* (MO, US). Boquete, Llanos Francia, 3300 ft, *Stern et al. 1210* (MO, US). 3 mi S of El Volcán, 4000 ft, *Tyson 876* (FSU, MO). Nuevo California W of Volcán, *Tyson 6670* (MO, NA, PMA). 2 mi S of Puerto Armuelles, *Wilbur et al. 13584* (DUKE, MICH, MO). NE of Cerro Pando, NW of Nueva California, 1500 m, *Wilbur et al. 11011* (DUKE, MO). COCLÉ: El Valle de Antón, 600–1000 m, *Allen 1158* (MO), *2328* (US); *Carrasco 5* (MO, PMA); *Correa 313* (MO); *Croat 13315* (MO, NY); *D'Arcy & D'Arcy 6757* (F, MO); *Duke 12110* (MO, NY, REED); *Gentry 6869* (MO); *Lallathin 6003* (MO); *Lewis et al. 2538* (MO, SCZ); *Spellman et al. 599* (MO); *Tyson et al. 2453-A* (MO); *Weaver & Foster 1639* (DUKE, DUKE); *Wilbur et al. 15613* (DUKE); *Wilbur et al. 11146* (F, DUKE, MO, NY). VERAGUAS: Starling Island (River San Pablo), *Barclay 1072* (US). Isla de Uva, Contreras group, *Pittier 5110* (US).

3. **Kohleria tubiflora** (Cav.) Hanst.,[16] Linnaea 34: 442. 1865.

Gesneria tubiflora Cav., Icon. 6: 61, *pl. 584.* 1801. TYPE: Taboga, Panamá, *Nee* (MA, not seen; photos MO, US).

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[16] Only those names used for plants from Panamá have been included.

G. rhynchocarpa Benth., Bot. Voy. Sulphur 131. 1845. TYPE: Isthmus of Darién, *Barclay* (BM, not seen).
Isoloma rhynchocarpum (Benth.) Decne., Rev. Hort. 20 [sér. 3, 2]: 465. 1848.
I. tubiflorum (Cav.) Decne., Rev. Hort. 20 [sér. 3, 2]: 465. 1848.
I. hondense (Hook.) Decne. var. *warszewiczii* Regel, Gartenflora 3: 2. *pl. 74b*. 1854. TYPE: Chagras, *Warszewicz* (not seen).
Brachyloma rhynchocarpum (Benth.) Oerst., Cent. Gesn. 29. 1858.
Cryptoloma rhynchocarpum (Benth.) Hanst., Linnaea 29: 538. 1859.

Coarse suffrutescent *herbs* or weak *shrubs* growing in clumps; stems succulent, erect or decumbent, 4 cm to 2 m tall, unbranched, the internodes elongate, green or more commonly reddish to maroon with green lines, pilose to hirsute, trichomes with reddish articulations, the bracts of rhizome pink. *Leaves* opposite, ovate to oblong, often falcate, 4.0–22.8 cm long, 1.5–12.2 cm wide, the apex acute to acuminate, the base cordate, rounded to acute, sometimes oblique, the margin crenate serrate, occasionally reddish, above dark green, pilose with appressed hairs, becoming scabrous, below light green in shade plants to dark red or purple in exposed plants, some plants green, others red in the same population, villous especially along the prominent veins, petioles sulcate, slender, 1.3–7.5 cm long, 1–2 mm wide, usually green on the upper side and reddish on the lower side, densely villous. *Inforescences* of 1–10 flowers per fascicle in the axils of the upper leaves, erect; peduncles lacking; pedicels surrounded by a few leaflike bracts at the base, nearly equalling the petioles in length, green to brownish, villous with patent hairs. *Flowers* brightly colored; floral tube globose or turbinate, ca. 4 mm in diam., accrescent in fruit, green, villous; calyx lobes erect, membranous, the tube short, ca. 1 mm long, lobes 5, equal, triangular to lanceolate, acute, all green or maroon tipped, villous; corolla bright red, orange, salmon red, or yellow orange, toward the apex becoming greenish or red outside, the inside light yellow, the tube 2.1–3.0 cm long, nearly straight from a rounded base, 3–4 mm in diam., ampliating to 6–9 mm near the middle, narrowing to 3–6 mm at the mouth, villous with reddish hairs outside, inside glandular, the lobes of the limb erect, rounded, 1–2 mm long, green or yellow with purple spots to reddish; stamens adnate to the base of the corolla tube, to 2.5 cm long, yellow, sparsely glandular, the anthers oblong, ca. 2 mm long and wide; glands 5, distinct; ovary apex conic, pilose, the style nearly straight, ca. 2 cm long, pilose, the stigma bilobed to clavate, glandular papillate. *Fruit* a green, yellow, or brown capsule, ovoid, globose or turbinate, to 1 cm long, the apex conic, opening by 2 valves; seeds tawny to reddish brown, fusiform, ca. 0.5 mm long. *Chromosomes* $n = 13$ (Davidse, 1970, based on material from Costa Rica.

Kohleria tubiflora is apparently the most commonly collected member of the Gesneriaceae in Panamá, known from the provinces of Coclé, Colón, Los Santos, Panamá, San Blas, Veraguas, as well as the Canal Zone. The species has been found in a variety of habitats from rocky banks in full sun to wet forests in total shade, including moist clearings or trailsides, sea cliffs, and newly burned areas. Beyond Panamá, *K. tubiflora* is known also from Costa Rica, Venezuela and Colombia.

The species is known as "Perrito" according to *Paul 161* (US).

CANAL ZONE: Barro Colorado Island, *Aviles 4* (MO), *82* (F); *Croat 4176, 4370* (both DUKE, F, MO, NY, SCZ), *6355, 6417* (both MO), *6951* (F, NY, SCZ), *11977* (MO, SCZ, US), *12280* (F, MO, SCZ), *12579* (MO); *Foster 1367* (F, DUKE, PMA); *Killip 40023* (US); *Standley 40819* (US); *Weaver & Foster 1621* (DUKE); *Wetmore & Abbe 30* (F, MO). Cerro Viejo on K16C, *Blum 1238* (FSU, MO, SCZ). Fort San Lorenzo, *Burch et al. 1039* (DUKE, MO, SCZ). Road S-10 N of Escobal, *Croat 12441* (MO). Pipeline Road within 5 mi of Gamboa Gate, *D'Arcy 9284* (MO). Front of Summit Garden, *D'Arcy 9304* (MO). Sosa Hill, *Duke 4663* (MO, US). K-6 Road, *Dwyer 3031* (MO). Madden Dam, *Dwyer 5050* (MO). Hill opposite Paraíso Development, Paraíso, *Dwyer 7142* (MO, NY, US). Road K-19, 2 mi from W border of Zone to cleared area near Canal, *Gentry 1782* (F, MO, NY, SCZ). Cerro Galera 2 km from Pacific Ocean near boundary of Canal Zone, 350–400 m, *Gentry 6646* (MO, PMA). Ancón Hill, *Greenman & Greenman 5094* (MO). Between Summit and Gamboa, *Greenman & Greenman 5243* (MO). Near Las Cruces Trail, *Harvey 5036* (F). Cerro Ancón, *Heriberto 48* (US). Pipeline road near Río Agua Salud, *Kennedy & Redemsky-Young 1837* (MO). Ancón Hill, 100–200 m, *Killip 3001* (MO, NY, US), *12065* (PH, US). Behind Curundú, *Loftin* (SCZ). Navy Reservation N of Gamboa, *Maas & Dressler 717* (MO). Fort San Lorenzo, Fort Sherman Military Reservation, *Maxon & Valentine 7010* (US). Balboa, *Mell 13* (NY, US). Pipeline road 14.4 km from Chagres Airport road, 0–100 m, *Mori & Kallunki 2061* (MO). NW edge of Gamboa, *Mori & Kallunki 2221* (MO). Top of Cerro Pelado 1 km N of Gamboa, 200–220 m, *Nee 8824* (MO, US). End of "abandoned" road C-29 6 km E of Gamboa, 160–190 m, *Nee 8981* (MO, US). Panamerican Highway between Rodman Marine Base and Chorrera, *Nowicke et al. 3605* (MO). Ancón, *Paul 161* (US). Río Grande near Culebra, 50–100 m, *Pittier 2124* (US). Tributary of Río Frijole near Pipeline Road N of Gamboa, *Skog et al. 4001* (E, MO, P, US). Road K-9, *Smith & Smith 3267* (US). Ancón Hill, *Standley 25219* (US). Sosa Hill, Balboa, *Standley 25250* (US). Balboa, *Standley 25589* (US). Las Cascadas Plantation near Summit, *Standley 25695, 29637* (both US). Hills W of the Canal near Gatún, *Standley 27233* (US). Gamboa, 102.5 ft, *Standley 28314, 28514* (both US). Old Las Cruces Trail between Fort Clayton and Corozal, *Standley 29120* (US). Río Paraíso above East Paraíso, *Standley 29879* (US). Obispo, *Standley 31781* (US). Chiva Chiva Trail near Miraflores Lake, *Tyson 1408* (FSU, MO, SCZ). 4–6 mi N of Gamboa along Pipeline road, *Tyson 1490* (FSU, MO, SCZ). Old Fort San Lorenzo, *Tyson 2212, 2221* (both MO). 1 mi N of Summit Garden, *Tyson & Blum 1958* (SCZ). 1 mi N of Summit on road to FAA tower, *Tyson et al. 2748* (SCZ). Miraflores, *White & White 60* (MO, US). 1 mi SW of Cocolí in the Rodman Naval Ammunition Depot, *Wilbur et al. 12890* (DUKE). Across highway from Summit Garden, *Witherspoon & Witherspoon 8698* (MO). COCLÉ: El Valle, 800–1000 m, *Allen 743* (MO, NY). 1 mi from El Valle, *Garner 34* (DUKE, PMA, SCZ). El Valle, *Harvey 5147* (F). Llano Bonito, N of Las Margaritas, 400–500 m, *Seibert 645* (MO, US). COLOŃ: Portobelo, *D'Arcy 4067* (MO); *D'Arcy & D'Arcy 6687* (MO). Salamanca, *Gracia 3* (MO, PMA). Ca. 1 km S of Portobelo near sea level, *Nee & Gentry 8754* (MO, US). Portobelo, 0–20 m, *Pittier 2446* (US). Puente Viejo del Río de Puerto Pilón, *Taymes 16* (DUKE, MO, PMA). 5–7 mi SW of Portobelo towards María Chiquita, *Wilbur & Weaver 11204* (DUKE). DARIÉN: Boca de Pirre, *Bristan 1269* (MO). Airstrip at Caná gold mine, 480 m, *Croat 37978* (MO). 0–4 mi up Río Sabana from Santa Fé, *Duke 4134* (MO, US). Río Cucunatí at Puente Quemado, *Duke 8809* (MO). Río Sabana above Santa Fé, *Duke 14095* (MO). Yaviza, 50 m, *Gentry & Mori 13520* (MO). Upper Río Tuquesa, *Le Clezio 256* (MO). LOS SANTOS: Headwaters of Río Pedregal, 25 mi SW of Tonosí, 2500–3000 ft, *Lewis et al. 2909* (DUKE, MO). Between Tonosí and Macaracas, *Oliver et al. 3548* (MO). PANAMÁ: Road to Cerro Campana 1 mi W from Su-Lin Motel, 800 m, *Correa & Dressler 364* (PMA), *365* (MO). 3 mi above Interamerican Highway on road to Cerro Campana, *Croat 12050* (MO). Between Río Bayano Dam & Cañitas, *D'Arcy 9396* (MO). Edge of recently cut forest at bridge site ca. 4 mi S of Cañitas, *D'Arcy & D'Arcy 6055* (MO). Río Chagres 1 mi above Madden Lake, *Duke 4457* (MO, US). Rocky slope on Interamerican Highway 4 mi NW of Bejuco, *Duke 4562* (MO, US). Gallery along Río Torable, near Panamerican Highway and El Llano, *Duke 5656* (MO, SCZ). Panamá Viejo, *Duke 5718* (MO). Headwaters of Río Corso off Río Pacora, 500 m, *Duke 11926* (MO). Cerro Campana, beyond Motel Su-Lin, 2700–3000 ft, *Duke 8655* (MO). Cerro Azul, 2000 ft, *Dwyer 2797* (MO). Cerro Campana above Su-Lin Motel, 3000 ft, *Dwyer & Kirkbride 7820* (MO). Cerro Campana, *Ebinger 939* (F, MO, US). From first sharp bend on Río Pasiga, 0–2.5 mi along lumber road to Río Maestro, *Gentry 2319* (MO). Main beach, 8°15′N, 79°08′–79°09′W, San José Island, Pearl Archipelago, *Harlow 54* (US); *Johnston 125* (MO, US). East Bay, San José Island, *Johnston 171* (US). Cerro Campana, *Lewis et al. 3067* (MO, SCZ). Chimán, *Lewis et al. 3323* (MO, PMA), *3360*

(MO). Tributary of Río Chagres 5 mi SW of Cerro Brewster, 1000 ft, *Lewis et al. 3461* (MO). Cerro Campana 8.6 mi SW of Capira, *Luteyn 1052* (DUKE). Television tower on ridge (Cerro Penon), 3 km S of Alcade Díaz, 410–440 m, *Nee 8598* (MO, US). Sabanas N of Panama City, *Paul 506* (US). Upper Mamoní River, 150–400 m, *Pittier 4482* (US). Agricultural Experiment Station at Matías Hernández, *Pittier 6798* (US). Corozal Road, *Standley 26828* (US). Taboga Island, *Standley 27894* (US). Río Tapia, *Standley 28143* (US). Near Matías Hernández, *Standley 28927* (US). Cerro Azul, 2000 ft, *Tyson 2107* (MO). W slope Cerro Campana, 2500 ft, *Tyson et al. 2341* (FSU, SCZ). Mangrove swamp, Playa Grande, San José Island, Perlas Islands, *Tyson & Loftin 5089, 5094* (both FSU, MO, SCZ). Trail to Cerro Campana, *Witherspoon & Witherspoon 8908* (MO). SAN BLAS: Beach E of Puerto Obaldía, *Croat 16900* (F, MO). Mainland in front of Ustupo, *D'Arcy 9487* (MO). Hills of Sperdi near Puerto Obaldía, 20–200 m, *Pittier 4389* (US). VERAGUAS: Santa María River, ca. 5 mi N of Santiago, *Blum & Tyson 627* (SCZ). WITHOUT LOCALITY: *Bristan 1524* (NY); *Duke 1615* (MO); *Hayes 708* (NY).

16. MONOPYLE*

Monopyle Moritz ex Benth. in Benth. & Hook. f., Gen. Pl. 2: 997. 1876. TYPE: *M. leucantha* Moritz ex Benth. = *M. subdimidiata* (Klotzsch & Hanst.) Mansf.

Scoliotheca Baill., Bull. Mens. Soc. Linn. Paris 1: 724. 1888. TYPE: *S. trianae* Baill. = *Monopyle macrocarpa* Benth.

Terrestrial *herbs* from rhizomes; stems erect or decumbent, rooting from the lower nodes, terete, slender, often reddish, pubescent to pilose, the internodes short or to 3 cm long, seldom branched. *Leaves* opposite, usually unequal in a pair, sometimes appearing alternate by the reduction of one of the leaves in a pair; blades membranous, ovate, elliptic to obovate, the base usually strongly oblique, the margin serrate to doubly serrate, dark green, pilose to strigillose and often bullate or areolate above, below light green to deep purple, and pilose especially along the veins beneath, the lateral veins 6–8, arching toward the apex; petioles ⅙–½ the length of the blade, those of a pair joined across the stem in a stipular line, green or reddish, pilose. *Inflorescences* few, each terminating a stem, long pedunculate, cymose, racemose, umbellate, or paniculate, barely exceeding the subtending leaf; bracts linear, reduced; peduncles and pedicels slender, terete, green to reddish, densely glandular pilose. *Flowers* few to many, somewhat zygomorphic; calyx lobes 5, nearly equal, green to reddish, entire; corolla of 5 petals connate into an open-campanulate tube, oblique in the calyx, the base rounded, narrowed, or slightly saccate, with a flaring 5-lobed limb, white or white with blue especially at the limb, sometimes yellow in the throat; stamens 4, usually with a staminode, the filaments slender, curved inwardly, adnate to the base of the corolla tube, the anthers coherent, 2-celled, the cells divergent, the connective thick; disc much reduced or lacking; ovary subinferior, narrowly turbinate, pilose, the apex pubescent, the style thick, sparsely pubescent or glabrous, the stigma stomatomorphic, papillate, the ovules numerous on both the surfaces of the placental lamellae. *Fruit* a dry capsule, linear oblong, topped by the persistent calyx, opening by 1 or 2 longitudinal slits; seeds numerous, fusiform, striate.

Monopyle is a genus of about 15 species that occur from Guatemala south

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* See *Monopyle grandiflora* Wiehl., Selbyana 5: 88, 1978.

to Bolivia and east to Venezuela. The greatest concentration of species appears to be in Ecuador and Peru. Euglossine bees are suspected pollinators.

The closest genus to *Monopyle* is probably *Gloxinia*, but *Monopyle* may be distinguished by the anisophylly, oblique leaf bases, and the usually terminal inflorescences.

The generic name refers to the fact that the capsule often splits only on one side to let the seeds out a single opening.

Literature:

Morton, C. V. 1945. Las especies sudamericanas del género *Monopyle*. Revista Univ. (Cuzco) 87: 98–116.

a. Leaves, floral tubes, and calyx lobes green; floral tubes and calyx lobes densely covered with short, light yellow brown glandular, nonuncinate trichomes; calyx lobes 2–4 mm long, not recurved ..... 3. *M. panamensis*
aa. Leaves, floral tubes, and calyx lobes often purplish or reddish; floral tubes and calyx lobes sparsely to densely covered with eglandular trichomes of two lengths, uncinate, and longer straight trichomes; calyx lobes if less than 5 mm long, then recurved.
  b. Calyx lobes 2–6 mm long, usually recurved at apex, if more than 4 mm long, then sparsely pilose ..... 2. *M. maxonii*
  bb. Calyx lobes 5–15 mm long, not recurved at apex, if less than 10 mm long, then densely pilose ..... 1. *M. macrocarpa*

1. **Monopyle macrocarpa** Benth., Icon. Pl. 12: 85, *pl. 1198*, *fig. 1–5*. 1876, (excluding var. *isophylla* Benth.). TYPE: Tarapoto, Peru, *Spruce 4151* (K, holotype).—FIG. 23.

M. macrophylla Benth., Icon. Pl. 12: 86. 1876. TYPE: Colombia, *Lobb* (K, holotype).
Scoliotheca trianae Baill., Bull. Mens. Soc. Linn. Paris 1: 724. 1888. TYPE: Chocó & Barbacoas, Colombia, *Triana 2450* (P, holotype, US, photo; F, P, isotypes).
Monopyle pilosula Morton, Revista Univ. (Cuzco) 87: 112. 1945. TYPE: Between La Oveja and Quibdó, Dept. Chocó, Colombia, *Archer 1702* (US, holotype).

Terrestrial large *herbs*, *subshrubs* or slender *shrubs*; stems erect or ascending, 0.5–1.0 m tall, reddish to purple, densely pilose above, sparse below. *Leaves* strongly unequal; larger leaf in a pair oblong, elliptic, oblanceolate or obovate, 7–17 cm long, 3–8 cm wide, membranous, the apex acute to acuminate, the base oblique, subcordate to acute, the margin serrate, above usually more or less bullate, dark green, sparsely pilose to subscabrous, below green or purplish, sparsely to densely pilose especially along the veins; petioles 0.5–4.0 cm long, purplish, sparsely to densely pilose. *Inflorescences* of several flowers in terminal panicles, to 20 cm long; primary peduncles 5–9 cm long, reddish, pilose; bracts linear lanceolate, to 8 mm long, 1–2 mm wide, reddish, pilose; ultimate pedicels ca. 5 mm long at anthesis, elongating in fruit, reddish, pilose. *Flowers* with the floral tube slightly oblique to the pedicel, shortly cylindric. 2–3 cm long and wide, reddish, densely pilose with uncinate trichomes; calyx lobes linear to lanceolate, 5–15 mm long, 1–2 mm wide, elongating somewhat in fruit, erect, subsulcate, outside reddish, pilose with both uncinate trichomes and longer, larger, straight trichomes, inside lighter colored, nearly glabrous; corolla mostly white, the throat often yellow, the upper part or the base of the

FIGURE 23. *Monopyle macrocarpa* Benth.—A. Habit (×½). [After *Mori & Kallunki 6387* (MO).]—B. Flower (×9/10). [After *Skog & Folsom 4173* (US).]

tube purple or red spotted, or the limb pale purple, the tube oblique in the calyx, campanulate, 1.7–2.0 cm long, 3–4 mm wide at the base, ampliate to 1.0–1.5 cm broad at the throat, the outside pilose, the inside nearly glabrous, the limb lobes broadly rotund, erect to patent, 5–8 mm long, ca. 1 cm wide, entire; stamens included, the filaments curved, coiling after pollen is shed, adnate to the base of the corolla tube for 1 mm, ca. 8 mm long, glabrous, the anthers broadly sagittate, 2 mm long, all coherent at the apices, occasionally a short staminode present; disc lacking or much reduced; ovary apex conic, pilose, the style curved, 6–9 mm long, glabrous, the stigma stomatomorphic. *Capsule* cylindric, slightly curved, more or less gibbous on 1 side, 1.2–1.8 cm long, 3–4 mm in diam., brown to purple, pilose, dehiscent along 1 line on the side of the gibbosity; seeds irregular, broadly fusiform, ca. 0.5 mm long, the surface rugose, striate, dark reddish brown, attached to a thin white funiculus.

The plants of this taxon from the provinces of Coclé, Panamá and Darién closely resemble plants from Colombia and Peru and agree with the type of *Monopyle macrocarpa* collected by Spruce at Tarapoto, Peru. The plants from Panamá often have nearly completely white corollas, but the variation in corolla color of *Monopyle* species is quite wide. *Monopyle macrophylla* Benth. from Colombia is also included in this taxon. Since both names were published at the same time either could have been used, but I have selected *M. macrocarpa* Benth. as the name for the species for two reasons: the description of *M. macrocarpa* is more detailed and complete, and the flower and fruit characters are illustrated. The plant shown occupying most of *Plate 1198* is *M. macrocarpa* var. *isophylla* Benth., so far unknown to me from specimens and is therefore excluded from consideration here, but the floral dissections and fruit drawn near the edges of *Plate 1198* are of the typical variety. These same dissections are drawn on the type specimen of the typical variety. The characters of the two varieties are likewise intertwined in the description of the species, however, a careful reading elucidates what Bentham saw as the typical variety, and which I consider to be the same as that growing in eastern Panamá.

In Panamá, *Monopyle macrocarpa* has been seen mainly in 5 locations: in Coclé near El Valle and near El Copé, in Panamá northeast of Altos de Pacora, and along the El Llano-Cartí road, and in the province of Darién near the summit of Cerro Pirre. In all locations the plants grow in cloud forest on shady damp slopes.

COCLÉ: N of El Valle de Antón, 1000 m, *Allen 2928* (US). Alto Calvario, 7 km N of El Copé, 700–900 m, *Folsom 3246* (MO, US). El Petroso, 7 km beyond El Copé, 800 m, *Skog et al. 4212* (MO, US). DARIÉN: Cerro Pirre, *Bristan 461* (MO); *Duke 6596* (MO); *Duke & Elias 13789, 13825* (both MO); *Folsom 4379A, 4389B* (both MO); *Gentry & Clewell 6975, 7100* (both MO); *Mori & Kallunki 5479* (MO). PANAMÁ: Road to Cartí 19 km N of El Llano, 500 m, *Busey 888* (MO, NY). 3 mi NE of Altos de Pacora, 500–800 m, *Croat 22733* (US). El Llano-Cartí road, Gorgas Lab Mosquito Control Project Site at km 12, *Croat 26065* (MO). La Eneida, Cerro Jefe, *Dressler 3297* (PMA). El Llano-Cartí highway 10–20 km N of El Llano, 350 m, *Dressler 4245* (PMA); *Folsom et al. 1466* (US); *Liesner 1136* (US); *Kennedy 2529, 2565* (both MO); *Kennedy & Dressler 3337* (US); *Kennedy et al. 2428* (MO). 5–10 km NE of Altos de Pacora, on trail at end of road, 750 m, *Mori & Kallunki 4850* (US), *4950* (MO). El Llano-Cartí road, 11–18 km from

Panamerican Highway, 350 m, *Mori & Kallunki 5137* (MO, US), *6387* (MO); *Mori et al. 4557*, 1100–1200 ft, *4177* (both MO); *Nee & Dressler 9344* (MO); 600 m, *Skog & Folsom 4173* (E, MO, US).

2. **Monopyle maxonii** Morton, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1183. 1938. TYPE: Vicinity of La Palma, on the road to La Hondura, Prov. San José, Costa Rica, *Maxon & Harvey 7947* (US, holotype).

Large terrestrial *herbs* or *shrubs*, rarely epiphytic; stems more or less erect, 0.3–1.5 m tall, slender, ca. 5 mm in diam., purplish, sparsely pilose to glabrous; branches few or none. *Leaves* strongly unequal in a pair; elliptic or oblong, often falcate, 7–18 cm long, 3.5–9.5 cm wide, membranous, the apex acute to acuminate, the base oblique, cordate to acute, the margin serrate, above dark green, sparsely pilose, below lighter green or purplish, nearly glabrous but sparsely pilose along the prominent midvein; petioles 1.5–3.5 cm long, green to purplish, sparsely pilose; smaller leaves in a pair to 3.5 cm long, short petiolate. *Inflorescences* in the upper leaf axils or terminal, paniculate, to 20 cm long, with short side branches of several flowers; primary peduncles ca. 7 cm long, purplish, sparsely pilose, the bracts linear lanceolate, caducous, ca. 7 mm long; ultimate pedicels ca. 5 mm long at anthesis, elongating in fruit, purplish, pilose with uncinate trichomes. *Flowers* with the floral tube cylindric, 2–5 mm long at anthesis, the base rounded or gibbous, brown to purplish, densely puberulent with uncinate hairs and short glands; calyx lobes oblong or broadly triangular, 2–6 mm long, 1–2 mm wide, the apex rounded to acute, often recurved, entire, outside purplish, pilose, inside lighter, to yellow, more or less glabrous; corolla white at least at the base, above dark pink to purplish, the tube oblique in the calyx, campanulate, 1.4–1.8 cm long, 2–4 mm wide at the base, 1.1–1.8 cm wide at the throat, the outside pilose, the inside glabrous, the lobes of the limb nearly equal, subpatent, 3.8 mm long, entire, the stamens included, the filaments adnate to the base of the corolla tube, curved, ca. 1 cm long, glabrous, the anthers coherent by their apices into a square; disc lacking, ovary apex pilose, style ca. 1.2 cm long, glabrous, the stigma stomatomorphic. *Capsule* cylindric, curved at the base, 1.0–1.5 cm long, 3 mm in diam., reddish brown; seeds not seen. *Chromosomes* $n = 13$ (Lee, 1966a).

This species was originally described from Costa Rica where it is more common. In Panamá, *Monopyle maxonii* has been found in the provinces of Bocas del Toro, Chiriquí, and Veraguas, in cloud forests. The species is distinctive by its purplish recurved calyx lobes.

BOCAS DEL TORO: Between Criollo, just above Buena Vista, and Quebrada Higueron on Chiriquí Trail, *Kirkbride & Duke 797* (MO). CHIRIQUÍ: Trocha 3 de Noviembre between Alto de Guayabo and Paso de la Zorra, 1400–1600 m, *Dressler 5476* (PMA). On Chiriquí Trail between Quebrada Hondo and divide, *Kirkbride & Duke 917* (F, MO, NY, REED). VERAGUAS: Santa Fé, forested slopes of Cerro Tute, 3000 ft, *Allen 4350* (MO, US). Valley of Río Dos Bocas along road between Escuela Agricola Alto Piedra and Calovébora, 15.6 km NW of Santa Fé, 450–550 m, *Croat 27741* (MO). 15–20 km NW of Santa Fé between Escuela Agricola Alto Piedra and continental divide, 650–800 m, *Dressler 4736* (PMA). NW of Santa Fé 2.8 km from Escuela Agricola Alto de Piedra, *Mori & Kallunki 6215* (MO).

3. **Monopyle panamensis** Morton, Ann. Missouri Bot. Gard. 29: 58. 1942. TYPE: Panamá, *Allen 2413* (US, holotype; BH, US, isotypes).

Terrestrial *herbs*, to 70 cm tall; stem erect, somewhat zig-zag, reddish, puberulent, 3–5 mm in diam.; rhizome ca. 5 mm in diam., the scales reddish, pilose. *Leaves* usually unequal, the larger leaf in a pair elliptic to obovate, 10–20 cm long, 5–8 cm wide, the apex acuminate, the base oblique, rotund, the margin dentate to serrate, the upper surface dark green, hirsute, below lighter green, puberulent, the lateral veins 8–11 pairs, arching; petioles about ⅓ the length of the blade, pilose; smaller leaf in a pair ovate or broadly elliptic, 4–11 cm long, 2.5–5.0 cm wide, otherwise similar to the larger leaf. *Inflorescences* terminating the stem, paniculate, about equalling the longest leaf; peduncles terete, elongating with age, 3.0–8.2 cm long, tawny in dried specimens, glandular or eglandular pilose, the apex bibracteate; the bracts leaflike, linear, ca. 3 mm long, green, pilose; pedicels erect, 3–22 cm long, elongating in fruit, glandular pilose. *Flowers* showy; floral tube oblique on the pedicel, cylindric, 3–5 mm long, 2 mm in diam. at anthesis, glandular pilose, the base slightly gibbous; calyx lobes oblong, 2–4 mm long, 1–2 mm wide, erect, the apex rounded, not recurved, green outside, glandular pilose, inside glandular; corolla white at the base outside, purple or blue-spotted inside, above bluish at the limb, the tube oblique in the calyx, campanulate, 1.2–1.6 cm long, ca. 3 mm wide at the base, ampliate to 1.2 cm broad at the throat, the outside sparsely pilose to strigose, the inside glabrous, the limb lobes erect, nearly equal, rotund, ca. 5 mm broad, entire; stamens included, the filaments curved, ca. 8 mm long, adnate to base of the corolla tube for ca. 2 mm, glabrous, the anthers triangular, coherent by their apices into a square; disc lacking; ovary apex pilose, the style curved, 8–10 mm long, glabrous, the stigma stomatomorphic. *Capsule* cylindric, ca. 1.5 cm long, brown, glandular pilose; seeds not seen.

A rare species, *Monopyle panamensis* is known only from the hills near Cerro Campana. Since no collections have been made since 1941, the species may be extinct. It differs from its nearest relatives in the petioles and inflorescences being clothed in dense, light brown, glandular-pilosulus trichomes. The calyx lobes are the size of those in *M. maxonii*, but are not purplish or recurved.

PANAMÁ: Cloud forest, hills above Campana, 600–800 m, *Allen 1871* (MO, US). Cerro Campana, 1000 m, *Allen 2413* (BH, US).

17. MOUSSONIA

Moussonia Regel, Ind. Sem. Hort. Bot. Turic. [4]. 1847. TYPE: *M. elongata* Regel, presumed to be based on *G. elongata* sensu Martens and Gal., fide Wiehler, 1975 = *M. deppeana* (Schlecht. & Cham.) Hanst.

Kohleria Regel, sect. *Moussonia* (Regel) Fritsch in Engler & Prantl, Nat. Pflanzenfam. 4(3b): 179. 1894.

Pubescent *herbs*, *subshrubs* or *shrubs*; stems erect, branched, lacking rhizomes. *Leaves* opposite, petiolate, lanceolate, ovate or elliptic, the apex often

acuminate, the margin toothed. *Inflorescences* cymose, axillary, of few to many flowers; peduncles elongated or lacking. *Flowers* with the calyx lobes 5, varying from short and ovate to long and linear or lanceolate; corolla red, orange to yellow, tubular, broader at the middle from a narrow base and throat, the limb 5-lobed, each nearly equal and rounded; stamens 4, adnate to the base of the corolla tube, not exserted; disc annular; ovary semi-inferior, the apex conic, the stigma stomatomorphic. *Fruit* a dry, ovoid or ellipsoid capsule, dehiscing loculicidally into 2 valves; seeds small and numerous. *Chromosomes* $n = 11$ (Wiehler, 1975).

The genus *Moussonia* was for a long time considered a section of *Kohleria*, but is separated from that genus on the basis of chromosome number ($n = 11$ in *Moussonia*, $n = 13$ in *Kohleria*), the lack of rhizomes in *Moussonia*, but which are present in *Kohleria*, and an annular disc found in the flowers of all species of *Moussonia* rather than 5 separate glands as in *Kohleria*.

About 10 species of *Moussonia* are known only from Central America from México to Panamá. *Moussonia ampla* and *M. serrulata* are endemic Panamanian species found only in the province of Chiriquí.

The generic name *Moussonia* appeared in the rare 1847 seed list from the botanic garden of Zurich. It was published along with other genera of Gesneriaceae whose names appeared there for the first time. Although Regel cited no authority for the basionym of the type species of *Moussonia*, simply "*Gesnera* Auct.," one might assume that the basionym was *Gesnera elongata* Kunth, since that was the only valid combination at that time. However, since *Gesnera elongata* is now considered part of *Kohleria*, one would have to submerge *Moussonia* into *Kohleria*, leaving the generic concept of *Moussonia* without a name. This reasoning would follow the assumption that the basis of the generic name is the name of a species, so the genus goes along with the species. However, if the basis of a generic name is the concept embodied in the original description, a different type species must then be proposed.

The description of *Moussonia* was written by Regel from a garden plant grown from seeds originally sent from México by Deppe. The garden plant may have been labelled *Gesnera elongata*, a tentative but unpublished name given by Martens and Galeotti, but the plant and the species were certainly not the same as *G. elongata* Kunth (Wiehler, 1975).

The genus is named for J. R. A. Mousson (1805–1890), the president of the society of naturalists in Zurich at the time of Regel's residence there, and who published numerous papers on natural history.

Literature:

Stone, M. H. 1977. *Moussonia*. The Gloxinian 27(4): 18–22.

Wiehler, H. 1975. The re-establishment of *Moussonia* Regel (Gesneriaceae). Selbyana 1: 22–31.

a. Calyx lobes toothed, to 1.8 cm long; capsule ellipsoid, 1.2–1.7 cm long ..... 1. *M. ampla*
aa. Calyx lobes entire, to 0.7 cm long; capsule ovoid, ca. 1 cm long ..... 2. *M. serrulata*

1. **Moussonia ampla** L. Skog, Brittonia 30: 322. 1978. TYPE: Panama, *K. Utley 5670* (US, holotype; DUKE, MO, isotypes).

Shrubs; stems woody, erect, to 1 m tall, 5 mm in diam. 30 cm from the apex, the internodes brown to reddish, pilose hirsute. *Leaves* nearly equal in a pair, lanceolate, ovate to obovate, oblique, 4.2–9.3 cm long, 1.8–3.9 cm wide, membranous, the apex acute to acuminate, the base acute to cuneate, the margin serrulate, above dark green covered with more or less erect uniseriate trichomes of 2 lengths, below lighter green or reddish, strigose along the prominent veins; petioles densely pilose, 0.5–1.8 cm long. *Inflorescences* axillary of single flowers; peduncles, when present, slender to 1.5 cm long; bracts, often caducous, linear, to 1.8 cm long, reddish, pilose, rarely bearing an undeveloped flower in the axil; pedicels slender, 0.3–1.5 cm long, elongating in fruit, reddish, pilose. *Flowers* with the floral tube conic or oblong, 3–5 mm long, 3 mm in diam., the veins prominent, densely pilose; calyx 5-lobed, the lobes connate for only 1–2 mm above the floral tube, each narrowly triangular, ca. 1.8 cm long, 2–3 mm wide at the base, the apex acuminate, the lower lobes prominently toothed on the apical ½, the lateral lobes toothed on only one side (lower) or on both, the upper lobe entire or rarely toothed, the outside pilose, inside sparsely pilose, corolla deep red, tubular, slightly curved, 4 cm long, 5–7 mm wide at the base, ventricose at the middle, ca. 1.4 cm wide, narrowing to ca. 1 cm in diam. at the throat, the outside densely pubescent, the inside glandular, the limb 5-lobed, spreading, each lobe suborbicular, ca. 5 mm long and wide, toothed; stamens 4, with a staminode 5 mm long, not exserted, the filaments adnate to the base of the corolla for 1 mm, free part ca. 3.5 cm long, coiling after anthesis, base yellow, sericeous, glabrescent above, the anthers suborbicular, joined in 2 pairs by their sides, ca. 2 mm long and wide; disc annular, ca. 1 mm long; ovary apex broadly conic, densely pilose; style curved, ca. 4 cm long, pilose, more sparse toward the apex, stigma stomatomorphic, ca. 1 mm wide. *Fruit* a dry capsule, splitting into 2 valves, ellipsoid oblong, 1.2–1.7 cm long, 6–10 mm wide, the veins prominent; seeds numerous, fusiform, ca. 0.5 mm long, striate, twisted, dark reddish brown.

This rare species differs from its nearest relative, *Moussonia serrulata*, in having much longer and toothed calyx lobes, a dark red corolla to 4 cm long, and larger ellipsoid fruit.

CHIRIQUÍ: Recently opened ravine W of Las Nubes 5 km NW of Cerro Punta and towards Cerro Picacho, 2000–2100 m, *Wilbur & Luteyn 19384* (DUKE). 8 km W of Cerro Punta, Las Nubes, 6100–6400 ft, *Utley 5670* (DUKE, MO, US).

2. **Moussonia serrulata** (Morton) Wiehl., Selbyana 1: 25. 1975.—FIG. 24.

Kohleria serrulata Morton, Ann. Missouri Bot. Gard. 26: 309. 1939. TYPE: Panamá, *Woodson et al. 1009* (US, holotype; MO, NY, US, isotypes).

Terrestrial *subshrubs* or *shrubs*; stems erect, to 2 m tall, the internodes slender, terete, densely hirsute, glabrescent, the nodes thickened; branches numerous. *Leaves* equal or usually somewhat unequal in a pair, apparently falling soon, leaving a bare stem a short distance below the apex; lanceolate to

Figure 24. *Moussonia serrulata* (Morton) Wiehl. Habit (×⅜). [After *Allen 4748* (US).]

ovate, 2.6–12.4 cm long, 1.5–5.7 cm wide, membranous but appearing thick by the abundant strigose vestiture on both the surfaces, the apex acute to acuminate, the base acute or rounded, serrulate, above dark green, rarely scabrous, below lighter green; petioles to 2 cm long, densely pilose. *Inflorescences* in the upper leaf axils of 1–3 flowers; peduncles rare, when present to 1 cm long, pilose; bracts, when present, minute; pedicels slender, 8–16 mm long, densely pilose. *Flowers* with the floral tube campanulate, 3 mm long, 3 mm wide at the top, pilose; calyx lobes narrowly triangular, to 7 mm long, shortly connate at base, pilose, entire; corolla usually orange red, but varying from yellow to deep red outside, usually yellow within with orange stripes and/or spots, the tube not spurred, erect in the calyx, slightly ventricose above, 2.3–2.8 cm long, 3–5 mm wide at the base, becoming ca. 8 mm wide at the throat, the outside pilose, the inside glabrous, the limb lobes erect to porrect, semi-orbicular, ca. 3 mm long, 5 mm wide, toothed; stamens reaching the corolla limb, the filaments adnate to the base of the corolla tube for less than 1 mm, to 2.5 cm long, pilose at the base,

glabrous above, the anthers with oblong locules, at anthesis coherent, becoming free; nectariferous ring glabrous; ovary apex conic, pilose, style ca. 2.0 cm long, the base sparsely pilose, glabrous above, the stigma stomatomorphic. *Capsules* ovoid, surrounded by the persistent sepals, ca. 1 cm long, 6 mm wide at the middle, pilose; seeds fusiform, a little less than 1 mm long, longitudinally striate, slightly twisted, tawny.

Moussonia serrulata is a somewhat weedy species known only from the province of Chiriquí which differs from most other species of *Moussonia* in the extreme reduction or absence of peduncles in most of the plants.

In the original publication of the species the collection number of the type specimen is given as *Woodson, Allen & Seibert 1609*. *1609* is clearly an error for *1009*; the holotype at US agrees in all details of the protologue including the herbarium accession number given by Morton, except for the collection number *1009*. It may be assumed that *1609* was a typographical error.

CHIRIQUÍ: Finca Lérida, upper slopes of Quebrada Velo, 5000 ft, *Allen 4748* (MO, NY, US). Volcán de Chiriquí, Boquete District, 7000 ft, *Davidson 957* (F). Cerro Colorado, 50 km N of San Félix, 1150 m, *Dressler 5129* (PMA). Boquete, Fred Collins Finca, 6000 ft, *Ebinger 730* (MO, US). Between Bajo Quiel and Bajo Mono 6 mi NW of Boquete, 1450 m, *Wilbur et al. 11968* (DUKE). Between Alto Quiel and the Río Caldera on the Bajo Chorro Trail near Finca Lérida, 9 mi NW of Boquete, 1700 m, *Wilbur et al. 15496* (DUKE). Bajo Mona mouth of Quebrada Chiquero along Río Caldera, 1500–2000 m, *Woodson et al. 1009* (MO, NY, US). Quebrada Velo, 1800 m, *Woodson & Schery 246* (MO, US). Finca Lérida to Peña Blanca, 1750–2000 m, *Woodson & Schery 328* (MO). Callejón Seco, Volcán de Chiriquí, 1700 m, *Woodson & Schery 509* (MO, US). Bajo Mona and Quebrada Chiquero, 1500 m, *Woodson & Schery 514* (MO, US).

18. NAPEANTHUS

Napeanthus Gardn., London J. Bot. 2: 13. 1843. TYPE: *N. brasiliensis* Gardn. = *N. primulifolius* (Raddi) Sandw.

Marssonia Karst., Fl. Colomb. 1: 97, *tab. 48*. 1860. TYPE: *M. primulina* Karst. = *Napeanthus primulinus* (Karst.) Benth. & Hook. f. ex Jacks.

Hatschbachia L. B. Smith, Anais Bot. Herb. "Barbosa Rodrigues" 5: 37. 1953. TYPE: *Hatschbachia reitzii* L. B. Smith = *Napeanthus reitzii* (L. B. Smith) Burtt ex Leeuw.

Terrestrial *herbs* from perennial rhizomes; stems usually short (Panamanian plants practically stemless), woody when present, decumbent and rooting at the nodes, green to brown, and pubescent. *Leaves* opposite, decussate, equal or subequal in a pair, the blades membranous to papyraceous, dry, linear lanceolate to oblong spathulate, usually somewhat falcate, the apex acute, acuminate, obtuse, or rounded, the base cuneate to subcordate, nearly entire or crenate serrate toward the apex, somewhat sinuate, green above, the mature leaves glabrescent, below lighter green, pubescent along the veins, stomata usually in groups, epidermal cells with nonundulating walls, the lateral veins 7–8, arching and anastomosing toward the margin and the apex; petioles lacking, with opposite blades joined by a line across the stem or short, green, pubescent. *Inflorescences* numerous, axillary, long persistent, pedunculate, cymose, subumbellate to racemose paniculate, often equalling the subtending leaf, occasionally shorter or longer with persistent small leaflike bracts; peduncles

and pedicels slender, terete to quadrangular, green, glabrescent. *Flowers* actinomorphic to zygomorphic, 1 to many per inflorescence, nodding before anthesis; calyx campanulate, rounded or turbinate at the base, of 5 equal sepals connate at the base up to ½ their length, green or rarely reddish, oblong, ovate, lanceolate or triangular, aestivation valvate, spreading in flower, in fruit erect and larger with prominent veins, persistent; corolla falling soon, of 5 petals connate from the base into a tube 1–2 times as long as the calyx, rotate or campanulate, sometimes ventricose, white to blue, pink or lilac, nearly glabrous, the limb spreading, the lobes imbricate in bud, usually entire but emarginate at the apex; stamens 5 and equal or 4 with a reduced sterile staminode and often didynamous, exserted or included, the filaments free from each other but adnate to the base of the corolla tube, the anthers orbicular or oblong, free, locules dehiscent by longitudinal slits, confluent at the apex; disc gland lacking; ovary superior, ovoid to globose, the style curved, persistent, the stigma slightly bilobed; ovules numerous on both the surfaces of the bilamellate placentae. *Fruit* a capsule included in the persistent calyx, oblong, ovoid or globose, 2- or 4-valved, the valves not persistent after dehiscence, the seeds light to dark brown, striate, shiny, ellipsoidal, the embryo straight.

About 16 species of *Napeanthus* occur from Guatemala south to Bolivia, east to the Guianas, and also in southeastern Brazil. Only one species is known in Panamá.

Literature:

Fritsch, K. 1925. Beiträge zur Kenntnis der Gesneriaceen I. Die Arten der Gattung *Napeanthus*. Sitzungsb. Akad. Wiss. Wien 134, Abt. 1: 121–127.

Leeuwenberg, A. J. M. 1958. Revision of *Napeanthus*. Acta Bot. Neerl. 7: 340–354.

1. **Napeanthus apodemus** J. D. Smith, Bot. Gaz. (Crawfordsville) 20: 6. 1895. TYPE: Llanos de Santa Clara, Jiménez, Comarca de Limón, Costa Rica, *J. D. Smith 5109* (US).—FIG. 25.

N. bullatus Wiehl., Selbyana 2: 110. 1977. TYPE: Steep banks near Río Agua Salud, N of Gamboa, Canal Zone, Panamá, *Dressler 4098* (SEL, holotype, not available for study).

Delicate terrestrial *herbs*; stems rarely over 2 cm tall, 3–5 mm in diam., terete, green to brown, pilose, glabrescent, unbranched. *Leaves* in a flat rosette, narrowly oblanceolate, elliptic, or obovate, usually somewhat falcate, 2.7–10.8 cm long, 1.2–4.2 cm wide, the apex rounded to acute, the base decurrent into the petiole, cuneate, or rounded, subentire to dentate or serrate, toothed especially toward the apex, the upper surface dark green, rarely bullate, sparsely pilose near the base, but glabrous toward the apex, the lower surface lighter green with stomatal groups appearing as whitish dots in dried specimens, pilose along the veins; petioles when present flattened, to 4 mm long, 1–2 mm wide, green, pilose. *Inflorescences* axillary, shorter or longer than the leaves, racemose to paniculate; peduncles long persistent, slender, terete to quadrangular, 1.7–3.6 cm long, green, pilose to glabrescent, the bracts leaflike, clasping the bases

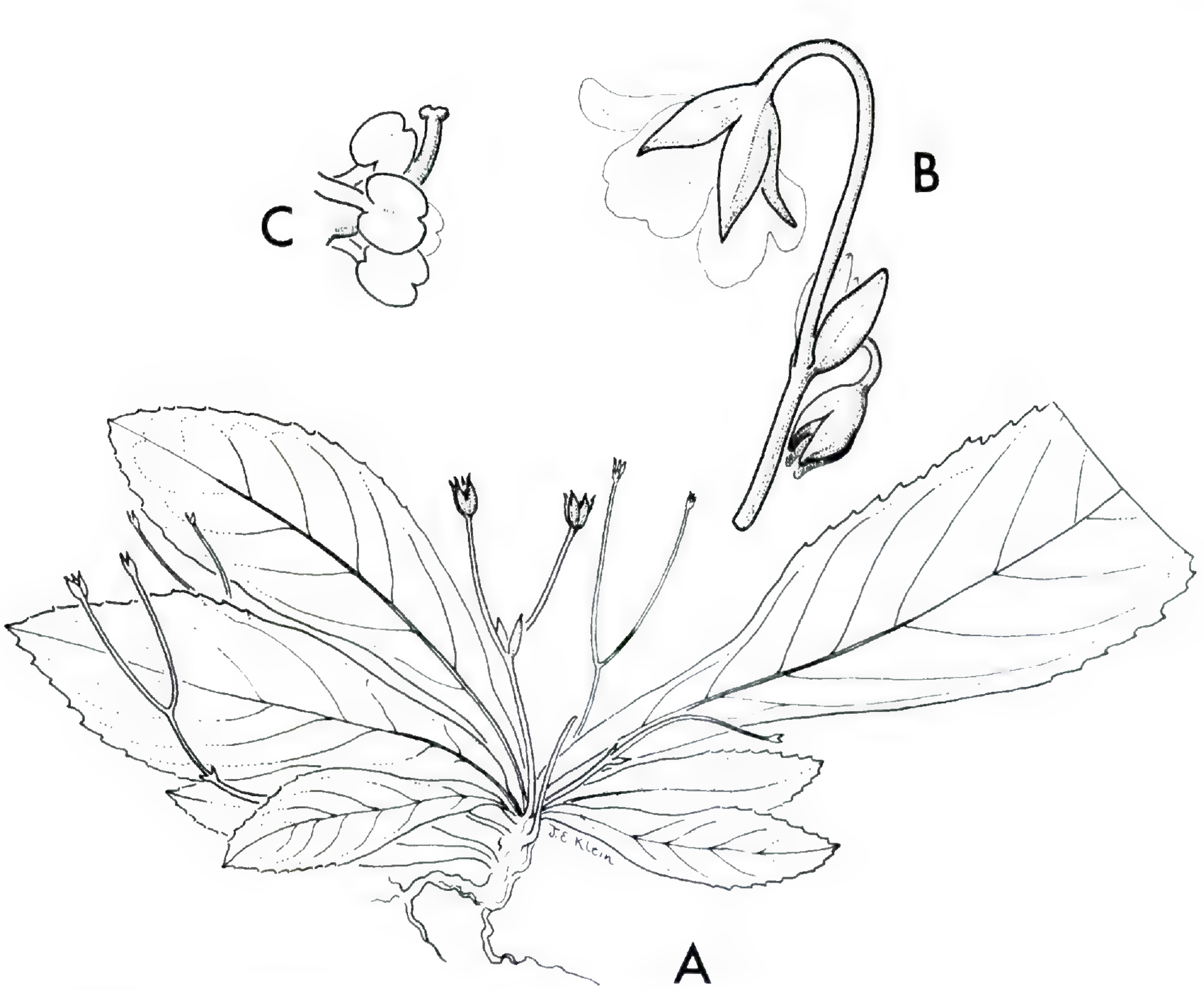

FIGURE 25. *Napeanthus apodemus* J. D. Smith—A. Plant with fruits (×7/10). [After *Croat 37683* (MO).]—B. Flower (×17/10).—C. Stamens and style (×69/10). [After *Skog et al. 4182* (US).]

of the pedicels, linear, 3–5 mm long, ca. 1 mm wide, green, pilose at least on the midvein beneath; pedicels often numerous 1–3 cm long, green, sparsely pilose. *Flowers* one to many; sepals joined at the base into a short tube, green to reddish, pilose at the base and along the prominent longitudinal veins above, the lobes 5, narrowly triangular or lanceolate, to 4 mm long, less than 1 mm wide to 3 mm wide, enlarging in fruit, the apex acute, the margin entire but pubescent; corolla caducous, usually white, rarely pale lavender or pink, glabrous, 4–6 mm long, rotate, the tube of 5 united petals, 1–2 mm long, the limb nearly regular, the lobes ovate, entire (?); stamens 4, inserted on the base of the corolla tube, the filaments 1–3 mm long, glabrous, the anthers orbiculate, ca. 1 mm broad, not coherent, locules divergent, yellow, the staminode ca. 1 mm long or less; ovary ovoid, ca. 1 mm long, yellow green, glabrous, the style curved, 2–3 mm long, glabrous, the stigma obscurely bilobed. *Fruit* a dry capsule surrounded by the persistent calyx, globose, 2–3 mm in diam.; seeds dark brown, shiny, fusiform, ca. 0.5 mm long, striate.

Few flowers were present on specimens from Panamá, and the description is mainly taken from holotype, *J. D. Smith 5109* (US), and *Skutch 4854* (US), both from Costa Rica.

Napeanthus apodemus occurs from Costa Rica through Panamá to Colombia in wet shady forests on steep slopes and often on stream banks. Plants are rare in Panamá and rarely collected anywhere. This species belongs to a complex which includes *Napeanthus subacaulis* (Griseb.) Benth. & Hook. f. ex Kuntze from Venezuela and Trinidad, *Napeanthus ecuadorensis* Fritsch from Ecuador, and *Napeanthus loretensis* L. Skog from Peru, and which may not be distinct.

The plants recently described as the new species, *Napeanthus bullatus* Wiehl., appear to be local variants of the widespread *N. apodemus*. Although none of the type material was available for study, other collections from the same areas fall into *N. apodemus*. Plants may have both acute and obtuse leaves. Young leaves are usually well clothed with trichomes on both sides; these trichomes tend to slough off during expansion of the blade. Occasionally one finds leaves with a few scattered trichomes remaining, especially on the lower side. Even the bullate condition is variable as noted in the discussion accompanying the original description of the new species. Amount of inflorescence investiture is variable throughout the range. No corollas were present on any of the specimens from the area of *N. bullatus* to examine the character of the margin. As no consistent differentiating character was seen, *N. bullatus* is included here as a synonym of *N. apodemus* J. D. Smith.

CANAL ZONE: Quebrada Lopez, 30 m, *Allen 2123* (MO). COCLÉ: 7 km N of El Copé, Alto Calvario, 700–850 m, *Folsom 4128* (MO, US). El Petroso 7 km beyond El Copé, 800 m, *Skog et al. 4203* (US). COLÓN: Between Agua Clara rain gauge and Puerto Pilón, *Dressler 3931* (PMA). Near Peluca, km 25.6 from Transisthmian Highway on the road to Nombre de Dios, *Kennedy 2670* (MO). Río Guanche, ca. 2.5 km upriver from bridge on road to Portobelo, *Mori et al. 6450* (MO). Santa Rita Ridge, *Mori & Kallunki 3042* (MO). Río Guanche 6 km S of Portobelo, 0–10 m, *Nee & Gentry 8720* (MO). Old logging road above Río Iguanita, 390 m, *Skog et al. 4182* (MO, US). DARIÉN: Gold mine at Caná, 500–600 m, *Croat 37683* (MO). Manené to mouth of Río Cuasí, *Kirkbride & Bristan 1391* (MO, NY, REED). Banks above Río Paca, *Stern et al. 592* (MO). Between Caná and Cuasí, Chepigana, *Terry & Terry 1471* (F, GH, MO). PANAMÁ: Tributary of Río Chagres 5 mi SW of Cerro Brewster, 1000 ft, *Lewis et al. 3425* (MO). El Llano Cartí-Tupile road 12 mi above Panamerican Highway, 200–500 m, *Liesner 1203* (MO). El Llano-Cartí road 12 km N of Panamerican Highway at El Llano, 400 m, *Nee 10476* (MO). SAN BLAS: Road from El Llano to Cartí-Tupile, Continental Divide to 1 mi from divide, 300–500 m, *Liesner 1299* (MO). VERAGUAS: Guabel (Río Dos Bocas), 16 km NW of Santa Fé, 500 m, *Dressler 4784* (PMA). Base of Cerro Tuti 6.5 km outside Santa Fé, *Folsom 3055* (MO). 16 km NW of Santa Fé on road to Calovébora, 300–500 m, *Mori & Kallunki 6145* (MO).

19. NAUTILOCALYX*

Nautilocalyx Linden ex Hanst., Linnaea 26: 181, 206–207. 1854. TYPE: *N. hastatus* Linden ex Hanst., nom. illeg. [*Centrosolenia bractescens* Hook.] = *Nautilocalyx bracteatus* (Planch.) Sprague.

Skiophila Hanst., Linnaea 26: 206–207. 1854. TYPE: *S. melittifolia* (L.) Hanst. = *Nautilocalyx melittifolius* (L.) Wiehl.

Episcia Mart., sect. *Skiophila* (Hanst.) Benth. in Benth. & Hook. f., Gen. Pl. 2: 1007. 1876.

Terrestrial or rarely epiphytic perennial *herbs* or low *shrubs*, occasionally

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* See *Nautilocalyx colonensis* Wiehl., Selbyana 5: 89, 1978; and *N. speciosus* Wiehl., Selbyana 5: 42, 1978.

producing tubers; stems erect or decumbent, succulent, sometimes rooting at the nodes. *Leaves* opposite, elongate, equal or unequal in a pair; blades lanceolate, elliptic or oblong, membranous or fleshy, often purplish below, the apex acute or acuminate, the base cuneate, often with a wing extending along the petiole. *Inflorescences* axillary of flowers in cymes, fascicles, or solitary, subtended by two or more leafy bracts. *Flowers* with an irregular calyx, the lobes unequal, green or colored; corolla white to yellow, usually with spots or lines of purple, tubular, broadened laterally, oblique in the calyx, with a short spur, limb 5-lobed, the lobes nearly equal, often large; stamens included, 4, filaments basally connate and adnate to the base of the corolla tube, the anthers apically joined in 2 pairs, dehiscing by a longitudinal slit; disc of a single posterior gland or of 2 opposite glands; ovary superior, the style included, the stigma bilobed. *Fruit* a bivalved capsule; seeds small, numerous, ellipsoid, striate, twisted.

Nautilocalyx includes more than 12 species found in the Lesser Antilles, in Central America from México to Panamá, and throughout northern South America from Peru to Colombia, Venezuela and the Guianas, and Amazonian Brazil. Three species occur in Panamá in damp, shaded situations.

This genus is perhaps most closely related to *Episcia* Mart., but differs in lacking stolons, a distinguishing character for *Episcia*.

The generic name may have been derived from an imagined similarity of the shape of the calyx to the shape of a chambered nautilus. No explanation of the name was given by either Linden or Hanstein.

Literature:

Batcheller, F. N. 1970. Gesneriads one by one: *Nautilocalyx*. The Gloxinian 20(3): 15–19.

Skog, L. E. 1974. Valid publication of *Nautilocalyx picturatus* [Gesneriaceae]. Baileya 19: 118–122.

Sprague, T. A. 1912. The genus *Nautilocalyx*. Bull. Misc. Inform. 1912: 85–90.

Wiehler, H. 1973. Seven transfers from *Episcia* species in cultivation (Gesneriaceae). Phytologia 27: 307–308.

a. Leaves oblanceolate, base of blade decurrent into petiole; calyx lobes narrowly lanceolate to linear ..... 1. *N. colombianus*
aa. Leaves ovate, elliptic to obovate, base of blade acute, rounded to cordate; calyx lobes lanceolate to ovate.
  b. Capsule oblong; style glabrous; leaf blades elliptic to obovate ..... 2. *N. dressleri*
  bb. Capsule globose; style pilose; leaf blades ovate ..... 3. *N. panamensis*

1. **Nautilocalyx colombianus** Wiehl., Selbyana 2: 113. 1977. TYPE: Along Río Guanche, SSW of Portobelo, Prov. Colón, Panamá, *Wiehler & Dressler 71160* (SEL, holotype, not available for study).

Terrestrial suffrutescent *herbs* or low *shrubs*; stems sprawling with tips ascending, to 1 m long, but usually ca. 0.3 m tall, succulent, ca. 8 mm thick, rooting from the nodes, the internodes green, densely pilose. *Leaves* subequal in a pair, oblanceolate or obovate, 10.5–34.5 cm long, 3.6–10.2 cm wide, membranous, the

apex acute to acuminate, the base cuneate to decurrent, dentate, crenate, or serrate, above green, pilose, below lighter green, densely pilose along the prominent veins; petioles 0.5–3.4 cm long, densely pilose. *Inflorescences* axillary, of 1–few flowers; peduncles when present very short; bracts linear, pilose; pedicels slender, 0.6–2.4 cm long, densely pilose; calyx lobes linear or narrowly triangular, 1.0–2.4 cm long, green, pilose; corolla white, oblique in the calyx, tubular, 2.5–4.5 cm long, the base spurred, ca. 5 mm in diam., broader above, to 1.5 cm wide at the throat, the outside pilose, the limb patent, lobes semiorbicular, to 1.5 cm long and wide, toothed; stamens included, the filaments 2–3 cm long, glabrous, coiling after anthesis; disc gland 1; ovary sericeous, the style glabrous, the stigma stomatomorphic. *Capsule* broadly ovoid surrounded by the persistent calyx, 6–9 mm long, 8–11 mm wide; seeds ellipsoid, striations deep, oblique, brown.

Nautilocalyx colombianus, known from Colombia and from the provinces of Colón, Darién, San Blas and the Canal Zone in Panamá, is probably closely related to *N. pictus* (Hook.) Sprague from Brazil and the Guianas.

CANAL ZONE: Quebrada Lopez, *Allen 2142* (MO, US). COLÓN: Near Guasimo along river, *Croat 9955* (MO). Río Guanche, 3–5 mi inland, 10–100 m, *Croat 26134* (MO), *26207* (MO). Between Agua Clara rain gauge and Puerto Pilón, *Dressler 3932* (PMA). Río Boqueron, 6–8 km upstream from Peluca Hydrographic Station, *Dressler 4658* (PMA). Road from Colón to Portobelo, Río Guanche, *Folsom 3766* (MO, US). Near bridge over Río Buenaventura near Portobelo, *Foster & Kennedy 1789* (DUKE, MO, PMA). Río Guanche, 2.5 km upriver from bridge on road to Portobelo, *Mori & Kallunki 3722* (MO). N side of Río Guanche, 1.5 km upstream from Puerto Pilón-Portobelo Highway bridge, 5–30 m, *Nee 7098* (MO). Above Río Iguanita, 390 m, *Skog et al. 4179* (E, MO, P, US). DARIÉN: La Boca de Pirre, *Bristan 1258* (US). Ascent for Cerro Pirre from Río Pirre S of El Real, 100–600 m, *Duke 5288* (MO). 10 mi S of El Real on Río Pirre, *Duke 5462* (MO, MO). Foothills of Cerro Coasí, headwaters of Río Cuasí, *Duke 15569* (US). Forest 1–3 m N of Paya, *Duke & Kirkbride 14017* (MO). S of El Real, headwaters of Río Pirre at a fork known as Dos Bocas, 100 m, *Foster & Kennedy 1250* (DUKE, MO, PMA). Río Pirre, 10 mi S of El Real Near 'Dos Bocas,' *Foster & Lowenbach 2264* (DUKE). Paya, Río Paya, *Stern et al. 402* (MO, US). SAN BLAS: Trail E of Cangandí-Mandinga airport road, 2–5 m S of Mandinga airport, *Duke 14814* (MO). Río Armila, 10 km WSW of Puerto Obaldía, *Mori et al. 6831* (MO).

2. **Nautilocalyx dressleri** Wiehl., Selbyana 2: 114. 1977. TYPE: Hills N of El Valle de Antón, Prov. Coclé, Panamá, *Dressler 4258* (SEL, holotype, not available for study).

Epiphytic or terrestrial *herbs*; stems succulent, erect or decumbent, the internodes densely pilose. *Leaves* nearly equal in a pair, obovate or elliptic, 7.5–18.0 cm long, 4.5–9.0 cm wide, membranous, the apex acute or acuminate, the base often oblique, acute or rounded, dentate, both sides green and pilose; petioles slender, 1.0–5.5 cm long, pilose. *Inflorescences* axillary, few-flowered; peduncles short; bracts ovate, 1–2.5 cm long, ca. 1 cm wide, entire, green, pilose; pedicels slender, ca. 2 cm long, pilose; calyx somewhat oblique, the lobes lanceolate or ovate, to 2.5 cm long, thin, the apex acute, the base subcordate, serrulate, light green, pilose; corolla white or cream with pink on the limb and in the tube, oblique in the calyx, the tube ca. 3 cm long, spurred at the base, ca. 7 mm in diam., slightly broader above, pilose, the limb 5-lobed; stamens included, the filaments coiled after anthesis; ovary pubescent, the style glabrous (fide Wiehler). Mature *capsule* not seen, oblong (fide Wiehler).

FIGURE 26. *Nautilocalyx panamensis* (Seem.) Seem. Habit (×½). [After *Killip 39974* (US).]

Nautilocalyx dressleri is very close to *N. panamensis* but differs in having larger bracts and a glabrous style among other characters. This species is known from damp forests in the province of Veraguas; specimens from Coclé have not been seen.

VERAGUAS: Río Dos Bocas ca. 12 km beyond Santa Fé, 450 m, *Croat 25786* (MO). Valley of Río Dos Bocas between Escuela Agricola Alto Piedra and Calovébora, 15.6 km NW of Santa Fé, 450–550 m, *Croat 27680, 27713* (both MO). Base of Cerro Tuti, 6.5 km outside of Santa Fé, *Folsom 3014* (MO, US).

3. **Nautilocalyx panamensis** (Seem.) Seem., Bot. Voy. Herald, Suppl. 250. 1854.—FIG. 26.

Scheeria panamensis Seem., Bot. Voy. Herald 185. 1854. TYPE: Panamá, *Seemann* 235 (BM, holotype; MO, photo).

Achimenes panamensis (Seem.) Hemsl. in Godm. & Salv., Biol. Cent. Amer., Bot. 2: 475. 1882.

Episcia inclinata T. S. Brandeg., Univ. Calif. Publ. Bot. 6: 63. 1914. TYPE: Finca Mexiquito, Chiapas, México, *Purpus 6851* (UC, holotype, not seen; MO, isotype).

E. panamensis (Seem.) Morton, Acta Bot. Venezuélica 2(2): 71. 1966.

Terrestrial *herbs*; stems succulent and brittle, erect, to 40 cm tall, the internodes reddish or green, pilose. *Leaves* nearly equal in a pair, more or less ovate, 6–19 cm long, 2.5–9.5 cm wide, thin, the apex acute to acuminate, the base acute, rounded or cordate, sometimes oblique, crenate to serrate, above light green, pilose, below lighter green, strigose along the veins; petioles slender, to 6 cm long, long pilose. *Inflorescences* axillary, of few-flowered clusters; peduncles lacking; pedicels to 2 cm long, pilose; calyx lobes resembling small leaves, free almost to the base, unequal, lanceolate to ovate, 1–2 cm long, serrate, green, pilose; corolla completely white, or white with pink lines in the tube, tubular, ca. 4 cm long, the base spurred, 3–5 mm wide, gradually broader to ca. 1 cm wide at the throat, linear grooves on the lower side of the tube, outside pilose, the limb somewhat spreading, lobes semiorbicular, 5–7 mm long, 7–10 mm wide, toothed; stamens at first nearly reaching the mouth of the corolla tube, after pollen shedding the filaments coiled, the anthers oblong, 1–2 mm long; gland single; ovary sericeous, the style glandular pilose, elongating as the filaments coil, 12–16 mm long; stigma bilobed. *Capsule* globose to oblate, ca. 1 cm wide, pilose; seeds ellipsoid to globose, surrounded at the base by fleshy funicle, striate, slightly twisted, dark brown. *Chromosomes* $n = 9$ (Wiehler, 1972, based on plants from México).

Nautilocalyx panamensis is common in the Canal Zone, especially on Barro Colorado Island, in open or shaded damp areas. The species is also found in the provinces of Darién and Panamá, as well as in México and Colombia.

CANAL ZONE: Barro Colorado Island, *Aviles 32* (F); *Bailey & Bailey 366* (BH); *Bangham 550* (F, US); *Croat 4126* (MO), *4338* (DUKE, F, MO, NY, SCZ), *6195* (F, MO, SCZ), *11678*, *11787* (both MO, US), *11814* (MO); *Ebinger 225* (F, MO, US), *568* (F, MO, NY, US); *Kenoyer 539* (US); *Killip 39974* (US); *Shattuck 221* (F, MO), *1168* (F, MO, US); *Standley 40810*, *41060* (both US); *Starry 34* (MO), *321* (MO, SCZ); *Weaver & Foster 1447* (DUKE, PMA). Cerro Viejo off of K16C, *Blum 1243* (FSU, SCZ). Madden Forest, Las Cruces Trail, *Gentry 1386* (MO, SCZ). Navy reservation N of Gamboa, Pipeline Road, marker 75, *Kennedy 460* (MO, PMA). 6 mi N Gamboa on ridge of Río Frijole, *Tyson 1522* (FSU, MO, SCZ). 5 mi NW Cocoli, 500 ft, *Tyson 1612* (SCZ). Pipeline Road, *Witherspoon & Witherspoon 8398* (MO, US), *8629* (MO). DARIÉN: Gold mine at Caná, 500–600 m, *Croat 37586* (MO). Cocalito near Panama-Colombia border, Pacific side, *Dwyer 4389A*, *4398B* (both MO). PANAMÁ: Tributary of Río Chagres 5 mi SW of Cerro Brewster, 1000 ft, *Lewis et al. 3401* (DUKE, MO, SCZ). Arenoso, lower Río Trinidad, 26–50 m, *Seibert 620* (MO, US).

20. NEOMORTONIA*

Neomortonia Wiehl., Selbyana 1: 17. 1975. TYPE: *N. rosea* Wiehl.

Epiphytic or cliff-dwelling *herbs*; stems pendent, slender, green or reddish, pubescent, frequently branched but not stoloniferous. *Leaves* opposite and decussate, rarely 3 at the node, small, ovate, obovate or elliptic, membranous, the apex acute or obtuse, toothed, green or reddish, glandular and pubescent; petioles short. *Inflorescences* axillary, infrequent, usually single-flowered; peduncles and bracts lacking; pedicels pubescent. *Flowers* with the calyx

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* See *Neomortonia nummularia* (Hanst.) Wiehl., Selbyana 5: 63. 1978.

lobes 5, free, green or reddish, pubescent; corolla oblique in the calyx, the tube spurred, infundibuliform, the limb 5-lobed; stamens 4, included; disc reduced to a single bilobed gland; ovary superior, the stigma stomatomorphic. *Fruit* an ovoid, laterally compressed berry; seeds striate, the base surrounded by an aril. *Chromosomes* $n = 9$ (Wiehler, 1975).

Neomortonia is a monotypic genus known from Costa Rica, Panamá, and Colombia, at low to high elevations in rain forests.

The plants resemble species of *Episcia* Mart., but differ mainly in being nonstoloniferous, and in having a berry fruit.

The genus name memorializes Conrad V. Morton (1905–1972), an eminent American botanist and student of ferns, Gesneriaceae, and other plant groups. He published a total of 267 papers of which 47 were on some aspect of the Gesneriaceae (Skog, 1974).

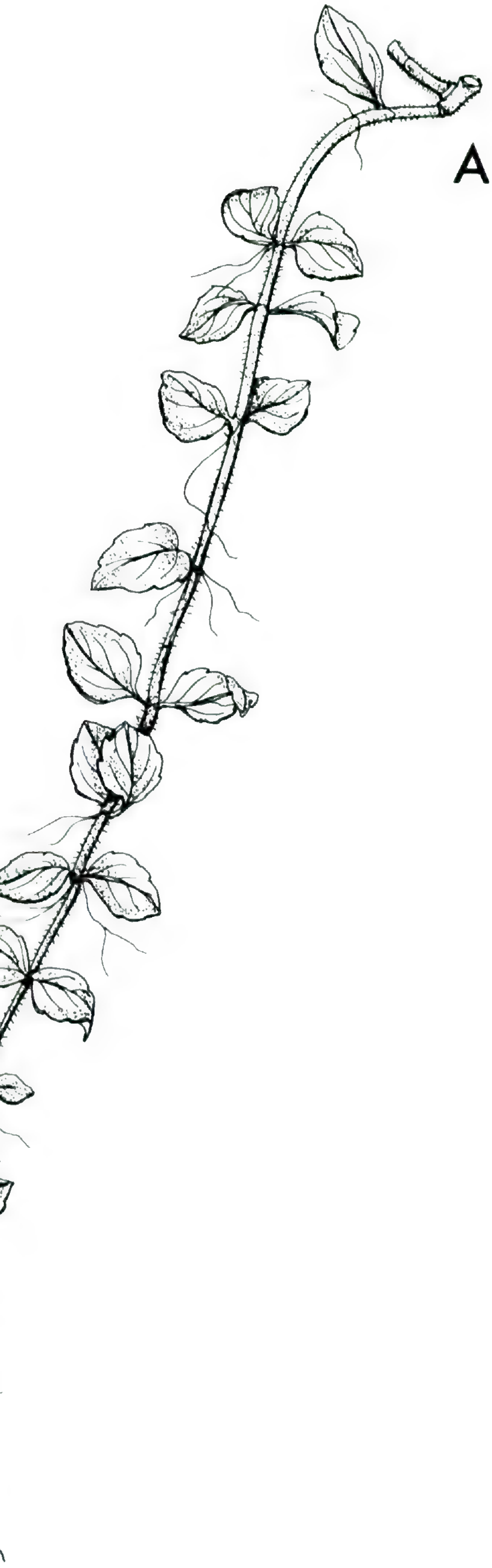
Literature:

Skog, L. E. 1974. Conrad Morton's publications on the Gesneriaceae. The Gloxinian 24(2): 33–35.

Wiehler, H. 1975. *Neomortonia*, a new genus in the Gesneriaceae. Selbyana 1(1): 16–21.

1. **Neomortonia rosea** Wiehl., Selbyana 1: 17. 1975. TYPE: Pacific slope of Cordillera Occidental, old road from Cali to Buenaventura, ca. 10 km W of La Elsa, Dept. El Valle, Colombia, *Wiehler et al. 7241* (US, holotype; MO, isotype).—FIG. 27.

Epiphytic or saxicolous *herbs*; stems pendent, repent, or scrambling, to 1 m long, slender, 1–2 mm in diam., green or reddish, strigillose, becoming gray brown in older branches; branches frequent. *Leaves* opposite decussate, rarely 3 at a node in a whorl, nearly equal in a pair; blades ovate or elliptic, 0.5–1.5 cm long, 0.5–1.0 cm wide, membranous, the apex acute to rounded, the base obtuse to acute, crenulate or serrulate, above green, puberulous, interspersed with scattered longer hairs, below green or pinkish, sparsely strigose; petioles 2–5 mm long, short pilose. *Inflorescences* axillary, of a single flower, the pedicels slender, ca. 5 cm long, green or reddish, sericeous. *Flowers* showy; calyx lobes distinct, lanceolate, 4–6 mm long, 1–2 mm wide, serrulate, green, pilose to sericeous; corolla white, with the upper part of the tube reddish pink, the inside orange or brown maculate, the tube oblique in the calyx, spurred at the base, funnel-shaped, ca. 1.5 cm long, narrowed above the spur, ca. 2 mm wide, then broader above to ca. 7–8 mm wide at the throat, the outside long pilose, the inside glandular pubescent, the limb slightly oblique, the lobes spreading to patent, suborbicular, each 5–6 mm long and wide, laciniate, glandular; stamens included, the filaments curved, 5–8 mm long, adnate to the base of the corolla tube, and briefly connate in a tube around the ovary, the anthers coherent in 2 pairs, each ca. 1 mm long, dehiscing by a longitudinal slit; disc reduced to a dorsal bilobed gland, white, glabrous; ovary pilose, the style glabrous, as long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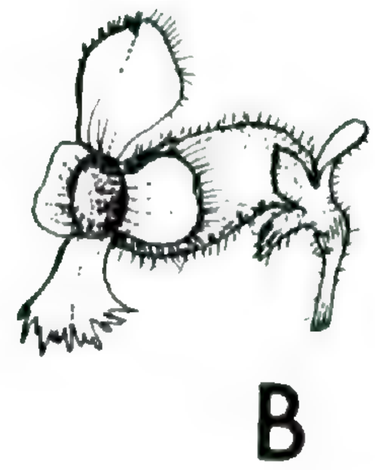
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as the stamens, the stigma stomatomorphic. *Berry* ovoid, laterally compressed ca. 1 cm long, orange, pilose; seeds fusiform, surrounded by an aril on lower ½, ca. 1 mm long, striate, yellow to brown. *Chromosomes* $n = 9$ (Wiehler, 1975).

This species is known from Costa Rica, Panamá, and Colombia in wet areas in rain forests. Although much more common in western Colombia, *Neomortonia rosea* has been collected a few times in Panamá.

Few flowers were present on specimens from Panamá, thus description of those parts in based on material from Colombia and the original description.

PANAMÁ: Río La Maestra, 0–25 m, *Allen* 5 (MO, MO, US). Logging roads, Río Pita, 1–3 mi above confluence with Río Maestra, *Duke 4751* (MO). DARIÉN: Elfin forest, Cerro Campamiento (S of Cerro Pirre), *Duke 15715* (US).

21. OERSTEDINA

Oerstedina Wiehl., Selbyana 2: 115. 1977. TYPE: *O. cerricola* Wiehl.

Epiphytic *herbs* or *subshrubs*; stems perennial, erect or ascending, pubescent toward the apex, the internodes often elongate, branching below. *Leaves* opposite and decussate, nearly equal in a pair, petiolate, more or less elliptic, often colored below, pubescent. *Inflorescences* densely clustered in the upper leaf axils; pedicels short or lacking, bracts present; pedicels short, pubescent. *Flowers* inconspicuous; calyx lobes 5, nearly equal, divided completely or nearly to the base, erect, often reddish, pubescent; corolla white with reddish spots, or pink, tubular, the tube inflated, gibbous at the base, barely exceeding the calyx lobes, the limb 5-lobed, the lobes more or less spreading; stamens included, the filaments adnate to the base of the corolla tube, free above; disc reduced to a single bilobed posterior gland, or occasionally with accessory glands; ovary superior, the stigma stomatomorphic. *Fruit* a berry, acuminate; seeds numerous, oblong, striate, reddish.

Oerstedina closely resembles *Rufodorsia* Wiehl., but differs in having an apically pointed fruit versus a laterally compressed or globose berry in *Rufodorsia*. The corollas in species of *Rufodorsia* have the 2 upper lobes dark red, whereas in *Oerstedina* the corolla is all white, reddish or with pink spots, or all pink.

Three or more species are included in *Oerstedina*, 2 from Panamá and Costa Rica and another from México. All occur at middle elevations in cloud forests.

Oerstedina was named for A. S. Oersted (1816–1872) a botanist from Denmark who, between 1845 and 1848, collected extensively in the West Indies and Central America (Costa Rica and Nicaragua). Among his many publications, his best known in the Gesneriaceae, *Centralamericas Gesneraceer*, was published in 1858 and included many new genera and species.

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FIGURE 27. *Neomortonia rosea* Wiehl.—A. Habit (×⅘). [After *Duke 4751* (MO).] —B. Flower (×1⅕). [After *Allen 5* (MO).]

a. Corollas 1.1–1.3 cm long; calyx lobes 5–8 mm long; petioles 1.3–2.8 mm long ..... 1. *O. cerricola*

aa. Corollas ca. 2 cm long; calyx lobes 1.0–1.2 cm long; petioles 2–5 cm long ..... 2. *O. suffrutescens*

1. **Oerstedina cerricola** Wiehl., Selbyana 2: 116. 1977. TYPE: Cultivated, Marie Selby Botanical Gardens from material originally collected in Prov. Chiriquí, Panamá, *Wiehler 77120* (SEL, holotype, not available for study).—FIG. 28.

Epiphytic *herbs* or *subshrubs*; stems fleshy, erect or ascending, 0.4–1.5 m tall, 4–8 mm in diam., the internodes elongate, to 8 cm long, green or more usually dark red to purple, densely pilose to sericeous or strigose above, less dense to glabrescent below; branching from the base. *Leaves* nearly equal in a pair, elliptic, 5–13 cm long, 1.5–5.0 cm wide, membranous, but thick from dense trichomes, the apex acute to acuminate, the base cuneate or decurrent into the petiole, subentire to serrulate, above dark green, strigillose, strigose to pilose, below green to dark red or purple, sparsely to densely strigose or strigillose, the veins prominent, reddish; petioles 1.3–2.8 cm long, reddish, strigillose to pilose. *Inflorescences* of dense cymes of 2 to several flowers; peduncles short or lacking; bracts lanceolate, 6–10 mm long, strigose to sericeous; pedicels 5–10 mm long, green or reddish, strigose to sericeous. *Flowers* inconspicuous; calyx lobes erect, free nearly to the base, lanceolate or oblong, 5–8 mm long, 2–3 mm wide, green to dark red, or pink, pilose to strigose or sericeous; corolla white with pink or purplish spots or all pink, the tube oblique in the calyx, 1.1–1.3 cm long, gibbous on the upper side at the base, ca. 3 mm wide below, ventricose at the middle, contracted just at the throat, the outside glabrous below, sericeous above, the inside glandular pubescent, the limb lobes spreading to patent, nearly equal, rotund, 2–3 mm long and wide, erose to subentire; stamens included, the filaments curved, adnate for ca. 2 mm to the base of the corolla tube, ca. 7 cm long, reddish, pubescent, the anthers coherent in 2 pairs by their apices, ca. 1 mm long, 1.5 mm wide; disc reduced to a posterior bilobed gland; ovary sericeous, the style ca. 1 cm long, reddish, glabrous, the stigma stomatomorphic. *Berry* ovoid, 4–5 mm long, 3 mm in diam., sparsely strigose to sericeous at the apex; seeds fusiform, ca. 1.5 mm long, 0.5 mm wide, longitudinally striate, dark reddish brown.

This species is quite variable in leaf coloration and amount of indumentum, but the flowers of the specimens most dissimilar in foliage are nearly identical.

Oerstedina cerricola occurs at mid-elevations in cloud forests in the provinces of Bocas del Toro and Chiriquí.

BOCAS DEL TORO: Róbalo Trail, N slopes of Cerro Horqueta, 6000–7000 ft, *Allen 4944* (MO). E slope of La Zorra to divide, *Kirkbride & Duke 814* (MO, NY). CHIRIQUÍ: Cerro Colorado, road 31.6 km beyond bridge over Río San Félix, 1690 m, *Croat 37142, 37162* (both (MO). Trocha 3 de Noviembre, between Alto de Guayabo and Paso de la Zorra, 1400–1600 m, *Dressler 5473* (Dressler coll.). Cerro Colorado, 1500–1750 m, *Folsom et al. 4671* (MO, US), *4678* (MO, US). Cerro Colorado, road to Bocas del Toro, *Folsom et al. 4788* (MO, US). Between Pinola and divide on Chiriquicito-Caldera Trail, *Kirkbride & Duke 854* (MO, REED). Ridge E of Cerro Horqueta, 1700–1900 m, *Luteyn & Wilbur 4614* (DUKE). Cerro Colorado 50 km N of San Félix on the continental divide, 1200–1500 m, *Mori & Dressler 7877* (MO). N of San Félix at Chiriquí-Bocas del Toro border, 5000–5500 ft, *Mori & Kallunki 5857* (MO, US).

FIGURE 28. *Oerstedina cerricola* Wiehl. Habit (×⅘). [After *Folsom et al. 4678* (MO).]

2. **Oerstedina suffrutescens** L. Skog, Brittonia 30: 324. 1978. TYPE: Panamá, *Mori & Kallunki* 5287 (MO, holotype).

Subshrubs; stems erect, to 1 m tall, ca. 5 mm in diam. at 15 cm below the apex, reddish, densely white sericeous near the apex, brownish gray and

glabrescent below, the internodes 1–2 cm long. *Leaves* nearly equal in a pair, elliptic to obovate, subfalcate, 8–15 cm long, 3–6 cm wide, membranous, the apex acute to acuminate, the base acute or cuneate, oblique, crenate serrate, above dark gray green, strigose, below lighter green, pilose to hirsute; petioles 2–5 cm long, 2 mm thick, dark green or reddish, villous. *Inflorescences* congested in the upper axils, cymose; peduncles short or lacking; bracts lanceolate, ca. 1.5 cm long, 2 mm wide, serrulate, pinkish, sericeous; pedicels to 7 mm long, pink, sericeous. *Flowers* with the calyx lobes equal, erect, free to the base, lanceolate, 1.0–1.2 cm long, 2–3 mm wide at the base, pink, sericeous but glabrous at the inner base; corolla white, nearly erect in the calyx, the tube subarcuate, 1.9 cm long, slightly gibbous at the base, ca. 4 mm in diam., subventricose above the middle, ca. 7 mm in diam., slightly constricted at the throat, the outside sericeous, the inside glandular especially at the throat, the limb spreading, the lobes suborbicular, the lateral and the basal lobes 4 mm long and wide, the upper lobes 2–3 mm long, the margin suberose; stamens included, the filaments 1 cm long, adnate to the base of the corolla tube for ca. 4 mm, free above but flattened toward the base, ca. 1 mm wide, and terete above, reddish, pilose at the base, glabrous above, coiling after anthesis, the anthers broader than long, 1 mm long, 2 mm wide; disc reduced to a single deeply bilobed posterior gland; ovary ovoid, strigillose, the style 1.3 cm long, red, glabrous, stigma scoop-shaped, erose. *Fruits* and seed not seen.

Oerstedina suffrutescens differs from the other species of *Oerstedina* in Panamá in having larger corollas, ca. 2 cm long; longer calyx lobes, 1.0–1.2 cm long; and longer petioles, 2–5 cm long. *Oerstedina cerricola* has corollas 1.1–1.3 cm long, calyx lobes 5–8 mm long, and petioles 1.3–2.8 cm long.

This species is known only from a single collection in the province of Veraguas in cloud forest on Cerro Tute.

VERAGUAS: Cloud forest on ridge top below summit of Cerro Tute, NW of Santa Fé, 2 km from Escuela Agricola Alto de Piedra, *Mori & Kallunki 5287* (MO).

22. PARADRYMONIA*

Paradrymonia Hanst., Linnaea 26: 180, 207. 1854. TYPE: *P. glabra* (Benth.) Hanst. = *P. ciliosa* (Mart.) Wiehl.

Trichodrymonia Oerst., Cent. Gesn. 38. 1858. TYPE: *T. congesta* Oerst. = *Paradrymonia congesta* (Oerst.) Wiehl.

Episcia Mart. section *Paradrymonia* (Hanst.) Leeuw., Meded. Bot. Mus. Herb. Rijks Univ. Utrecht, 146: 311. 1958.

Epiphytic or terrestrial *herbs* or *subshrubs*; stems erect, ascending, or scrambling, often succulent, bearing adventitious roots. *Leaves* equal to strongly unequal in a pair, often appearing to be in a rosette, but usually large, elongated and surpassing the stem; usually lanceolate, membranous to fleshy, the apex acuminate, the base cuneate or long decurrent into the petiole. *Inflorescences* of many flowers, usually congested into axils of the leaves, but rarely exceeding

* See *Paradrymonia alba* Wiehl., Selbyana 5: 46, 1978.

the length of the petiole. *Flowers* often hidden by the leaves; calyx lobes linear or lanceolate, free and usually long attenuate at the apex; corolla white or yellow with red or purple spots or lines, funnelform or trumpet shaped, spurred at the base; stamens included, the anthers oblong, coherent, bearded or not, dehiscing by a longitudinal slit; disc reduced to 1 or 2 glands; ovary superior. *Fruit* a bivalved capsule.

The 15 or more species of *Paradrymonia* appear to form a group distinctive by their often long, lanceolate leaves, congested axillary flowers, and usual rosette habit. They occur in Central and northern South America.

The generic name alludes to the resemblance of *Paradrymonia* to *Drymonia* Mart.

Literature:

Batcheller, F. N. 1976. Gesneriads one by one: *Paradrymonia*. The Gloxinian 26(1): 4–7.

Wiehler, H. 1973. Seven transfers from *Episcia* species in cultivation. Phytologia 27: 307–308.

a. Leaf blades glabrous above, usually reddish or brown.
  b. Calyx lobes linear or subulate, free to the base, ca. 1 mm wide, pilose; stems pilose; leaves less than 3 cm wide, or if wider then less than 15 cm long ..... 3. *P. lineata*
  bb. Calyx lobes lanceolate, free or united into a tube at the base, 3–10 mm wide, nearly glabrous; stems sericeous or sparsely strigillose above; leaves 6–25 cm wide, usually much more than 15 cm long.
    c. Corolla pale yellow; calyx lobes free to the base; leaves long decurrent, blades narrowly elliptic (6–18 cm wide), lacking a marginal vein .... 8. *P.* sp. B
    cc. Corolla reddish brown; lateral and basal calyx lobes united basally into a tube; leaves short decurrent, if at all, blades elliptic to ovate (10–25 cm wide), with a marginal vein ..... 7. *P.* sp. A
aa. Leaf blades pilose or strigose above, at least on the midvein, green to reddish.
  d. Inflorescences on long peduncles 10–14 cm long ..... 6. *P. pedunculata*
  dd. Inflorescences on short peduncles usually less than 2 cm long.
    e. Flowers densely congested in leaf axils, pedicels very short; calyx lobes pectinate to fimbriate ..... 4. *P. metamorphophylla*
    ee. Flowers not densely congested, but obviously pedicellate, pedicels 0.5–2.0 cm long; calyx lobes entire to serrulate.
      f. Anthers bearded; corollas reddish puberulent outside ..... 1. *P. decurrens*
      ff. Anthers not bearded; corollas whitish pilose outside.
        g. Leaves coarsely or double serrate, narrowly elliptic; corollas with a purple "eye" ..... 5. *P. ommata*
        gg. Leaves entire to serrulate, elliptic to broadly elliptic; corollas white with maroon stripes and spots ..... 2. *P. hirta*

1. **Paradrymonia decurrens** (Morton) Wiehl., Phytologia 27: 308. 1973.—FIG. 29.

Centrosolenia decurrens Morton, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1158. 1938. TYPE: Finca Montecristo, on the Río Reventazón below Cairo, Prov. Limón, Costa Rica, *Standley & Valerio 48589* (US, holotype).
Episcia decurrens (Morton) Leeuw., Acta Bot. Neerl. 8: 53. 1959.

Epiphytic *herbs* or *subshrubs*; stems creeping or scandent, to 0.5 m long, ca. 5 mm thick, succulent, the apex green or reddish, hirsute, becoming

FIGURE 29. *Paradrymonia decurrens* (Morton) Wiehl. Habit (×⅜). [After *Dressler 4552* (MO).]

gray brown below, the internodes often elongated, the nodes slightly swollen. *Leaves* strongly unequal in a pair, much exceeding the stems, the larger leaf in a pair elongate, oblanceolate or narrowly elliptic, 12–24 cm long, 2–10 cm wide, succulent to membranous, the apex long acuminate, the base cuneate, long decurrent into the petiole, remotely serrate or serrulate, above dark green, sparsely to densely long hirsute to strigose or sericeous, the hairs sometimes reddish on young leaves, below lighter green, hirsute to strigose; petioles elongated, 5–18 cm long, green or reddish, strigose to sericeous; smaller leaves linear, to 5 cm long. *Inflorescences* axillary, subumbellate, of many flowers; peduncles

short or lacking, the bracts linear, ca. 1 cm long; pedicels slender, 1–2 cm long, green or reddish, strigillose to hirsute. *Flowers* with the calyx lobes nearly equal, free, linear or subulate, 0.8–1.5 cm long, 1–2 mm wide, the margin remotely toothed or entire, green with reddish apices, often clothed with reddish pilose hairs; corolla white, creamy yellow or yellow, with reddish or transparent hairs outside, trumpet-shaped, spurred at the base, oblique in the calyx, the tube to 4 mm long, ca. 3 mm in diam. near the base, ampliate ventricose at the middle, ca. 9 mm in diam., slightly narrower toward the limb, the inside glandular, the limb lobes rotund, ca. 4 mm long and wide, the upper and the lateral lobes spreading, entire to erose, the basal lobe erect, toothed to fimbriate; stamens included, the filaments 2–8 cm long, adnate to the base of the corolla tube for ca. 4 mm, coiled after anthesis, glabrous, the anthers coherent, the cells divergent, 1–2 mm long, the apex bearded; disc reduced to a single dorsal gland; ovary reddish, villous, the style 2–3 cm long, sparsely pilose, the stigma broadly stomatomorphic. *Capsule* globose, ca. 5 mm in diam., green to cream colored, appearing red from the red-villous hairs; seeds fusiform to oblong, ca. 0.5 mm long, striate, dark reddish brown. *Chromosomes* $n = 9$ (Lee, 1964, as *Centrosolenia decurrens* Morton).

Paradrymonia decurrens can be found scrambling on trees or over dead logs or stumps, seldom more than 2 m above the ground, in wet forests at low elevations. The bearded anthers are a distinctive character for this species. Described originally from Costa Rica, the species is apparently more common in Panamá, found in the provinces of Bocas del Toro, Coclé, Colón, Panamá, and Veraguas.

BOCAS DEL TORO: Cerro Bonyic above Quebrada Huron, 500–1200 ft, *Kirkbride & Duke 599, 627* (both MO). Fish Creek Mountains, Chiriquí Lagoon, *Wedel 2238, 2270* (both MO), *2279* (MO, US). COCLÉ: La Mesa above El Valle, *Dwyer 11863* (MO); *Gentry 6841* (MO); *Nee & Dwyer 9160* (MO); *Skog & Butcher 4118* (MO, P, US); *Tyson & Godfrey 2425* (MO). COLÓN: 2–3 mi up Río Guanche, 10–20 m, *Kennedy & Foster 2126* (MO). PANAMÁ: El Llano-Cartí road, *Croat 26074, Croat 33745* (both MO); *Dressler 4552* (MO, PMA); *Mori & Kallunki 3517* (MO); *Mori et al. 4631* (MO); *Mori et al. 4140a* (MO); *Nee & Dressler 9355* (MO). VERAGUAS: Río Primero Brazo 2.5 km beyond Agriculture School Alto Piedra near Santa Fé, 700–750 m, *Croat 25489* (MO). Second branch of Río Santa María, road from Santa Fé, *Witherspoon & Dressler 8897* (MO, US).

2. **Paradrymonia hirta** L. Skog.[17] TYPE: Panamá, *Kirkbride & Duke 1293* (MO, holotype).

Herbs or *subshrubs*; stems trailing, decumbent, to 50 cm long, 2–3 mm in diam., bearing numerous adventitious roots, succulent, reddish and sericeous toward the apex, gray brown and glabrescent below. *Leaves* few (none complete); blades elliptic, ca. 12 cm long (?), 6–8 cm wide, fleshy, the base acute, cuneate to decurrent into the petiole, remotely serrulate or denticulate, ciliate, above dark green, nearly glabrous, but villous along the midvein, below lighter green or reddish, villous especially along the prominent reddish veins, glandular; petioles elongate, 5–12 cm long, 2 mm wide, reddish, sparsely to densely villous. *Inflo-*

[17] *Paradrymonia hirta* L. Skog, sp. nov. *Paradrymonia decurrens* (Morton) Wiehl. affinis, foliis villosis, antheris imberbis differt.

rescences axillary of 1 or few flowers; pedicels ca. 1 cm long, 1 mm in diam., red, villous; calyx lobes free to the base, lanceolate, 1.0–1.2 cm long, 1–2 mm wide at the base, remotely serrulate, red, villous, the lateral and the basal lobes erect, the upper lobe forced back by the corolla spur; corolla white with maroon stripes and spots, the tube nearly straight, funnelform, spur ca. 3 mm long, the tube to 3 cm long, 6 mm in diam. above the spur, 8–10 mm wide at the throat, the outside villous, the inside glandular, the limb bilabiate, the lobes ca. 8 mm long, pilose glandular, the margin ciliate glandular; stamens included, the filaments 2 cm long, glabrous above, the anthers not bearded, rectangular, 1 mm long and wide, coherent apically in 2 pairs, reddish on the back; style 2.2 cm long, pilose above, the stigma stomatomorphic. *Fruit* and seeds not seen.

This species is known in Panamá only from Darién Province, but it also occurs in northwestern Colombia. It most closely resembles *Paradrymonia decurrens* but lacks the bearded anthers of that species. As in other species of *Paradrymonia*, the habitat is wet forest.

DARIÉN: Cuasí-Caná trail between Cerro Campamiento and La Escalera to "Paramo" E of Tres Bocas, cloud forest and mossy forest, *Kirkbride & Duke 1293* (MO).

3. **Paradrymonia lineata** (Morton) Wiehl., Phytologia 27: 308. 1973.

Centrosolenia lineata Morton, Ann. Missouri Bot. Gard. 29: 41. 1942. TYPE: Panamá, *Allen 2717* (US, holotype; MO, isotype).
Episcia lineata (Morton) Leeuw., Acta Bot. Neerl. 8: 53. 1959.

Epiphytic *herbs* or *subshrubs*; stem short, to 20 cm long, fleshy, green and pilose but becoming woody and gray brown below with age, 0.5–1 cm thick. *Leaves* nearly equal to strongly unequal in a pair, erect, linear to elliptic, 10–24 cm long, 1.2–6.0 cm wide, succulent to coriaceous, the apex acuminate, the base cuneate to long decurrent, remotely denticulate, above dark green, glabrous, below pale green to pinkish, glaucous to sparsely strigose along the veins, the midvein prominent; petioles thick, 3–5 cm long, sparsely pilose. *Inflorescences* axillary, fasciculate, the flowers several per axil; peduncles lacking; bracts linear; pedicels slender, 3–20 mm long, reddish, sparsely pilose. *Flowers* sometimes hidden in the axils of the leaves; calyx lobes linear to subulate, free, 1.3–2.0 cm long, the anterior lobes longer, the posterior lobe reflexed by the corolla spur, green to reddish brown, long pilose to ciliate; corolla variously colored, off white, yellow or purplish outside, occasionally with reddish stripes, the inside yellowish or white with yellow area in the throat, or with maroon or purplish spots or stripes in the throat, the lobes white or yellow, sometimes purple flushed, the tube oblique in the calyx, spurred at the base, funnelform, 2.5–4.0 cm long, ca. 3 mm in diam. at the base, gradually ampliate above, not ventricose, outside sparsely pilose to glabrous, inside glandular pilose, the limb somewhat bilabiate, the lobes spreading, the basal lobe larger, to 1 cm long, the inside glandular pilose, the upper and the lateral lobes, ca. 5 mm long, more or less glabrous; stamens included, the filaments curved, adnate to the base of the corolla tube, glabrous, the anthers glabrous, coherent; disc reduced to a single

entire posterior gland; ovary pilose, the style glandular pilose, the stigma stomatomorphic. *Capsule* 2-valved, laterally compressed or globose, 4–5 mm in diam., pilose; seeds not seen. *Chromosomes* $n = 9$ (Lee, 1962, as *Episcia lineata*).

Paradrymonia lineata is distinguished by having narrow glabrous leaves, and striped corolla. It is most closely related to *P. lurida* of Costa Rica, which differs mainly in having the corolla lobes maroon spotted, and not glandular ciliate.

This species is known from the provinces of Coclé and Veraguas.

COCLÉ: El Valle de Antón, 900–1000 m, *Allen 2717* (MO, US); *Dressler 3048* (PMA); *Duke & Correa 14657* (MO); *Kennedy & Dressler 1746* (MO); El Petroso at Rivera's sawmill, 7 km beyond El Copé, 800 m, *Skog et al. 4197* (MO, US). VERAGUAS: Valley of Río Tercero Brazo beyond Escuela Agricola Alto Piedra above Santa Fé, *Croat 27325* (MO). 15–20 km NW of Santa Fé, between Escuela Agricola Alto Piedra and continental divide, 650–800 m, *Dressler 4743* (DUKE, F, PMA). 8.8 km from Escuela Agricola Alto de Piedra, *Mori & Kallunki 3255* (MO). NW of Santa Fé, 8.8 km from Escuela Agricola Alto de Piedra, Pacific slope, *Mori et al. 3961* (MO).

4. **Paradrymonia metamorphophylla** (J. D. Smith) Wiehl., Phytologia 27: 327. 1973.

Alloplectus metamorphophyllus J. D. Smith, Bot. Gaz. (Crawfordsville) 52: 52. 1911. TYPE: La Palma, Prov. San José, Costa Rica, *Tonduz 10884* (US, lectotype selected by C. V. Morton, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1145. 1938; specimen not found).

Herbs or *subshrubs*, the stems succulent to 1.5 m, at the apex white tomentose to lanate; glabrescent below. *Leaves* subequal to unequal in a pair, elliptic to ovate, 10–20 cm long, 3–9 cm wide, membranous, the apex acuminate, the base cuneate, serrulate, above dark green, pilose to sericeous, below lighter green or reddish, sparsely sericeous; petioles elongate, to 12 cm long, sericeous. *Inflorescences* densely congested in the leaf axils, corymbiform, of many flowers; peduncles ca. 1 mm long; bracts ovate, reddish, the margin fimbriate; pedicels short. *Flowers* with the calyx lobes erect, ovate to obovate, ca. 1 cm long, orange red, pilose to sericeous, more dense on the midvein, the margin pectinate to fimbriate; corolla reddish orange, infrequent or caducous, more or less erect in the calyx, the tube slightly spurred at the base, ca. 1.5 cm long, ventricose or broader at the middle and contracted at the throat, outside pilose toward the apex, glabrous below, inside glandular, the limb short, erect, the lobes nearly orbicular, ca. 2 mm long and wide; stamens included, the filaments curved, reddish, the anthers oblong, coherent; disc reduced to a single posterior gland; ovary pubescent, the style ca. 5 mm long, white, the stigma stomatomorphic. *Capsule* globose, ca. 5 mm in diam.; seeds not seen.

Paradrymonia metamorphophylla is unusual in having densely congested reddish inflorescences and nearly lanate stem apices. The species apparently occurs from Costa Rica to northern South America; in Panamá it has only been found in two places in the provinces of Bocas del Toro and Chiriquí, in cloud forest.

BOCAS DEL TORO: Róbalo Trail, N slopes of Cerro Horqueta, 6000–7000 ft, *Allen 4975* (MO, US). CHIRIQUÍ: Cerro Colorado, 1500–1750 m, *Folsom et al. 4670* (MO, US). Below divide on Chiriquicito-Calderas Trail, *Kirkbride & Duke 970* (MO, REED, SCZ).

5. **Paradrymonia ommata** L. Skog, Brittonia 30: 324. 1978. TYPE: Panamá, *Kirkbride & Duke 437* (MO, holotype; REED, SCZ, isotypes).

Herbs or *subshrubs*; stems erect to decumbent, upright part ca. 20 cm tall, becoming woody below and rooting at the nodes, slender, ca. 3 mm in diam. above, to 5 mm below, reddish, sparsely villous. *Leaves* nearly equal in a pair, lanceolate, narrowly elliptic to oblanceolate, 7–17 cm long, 1.2–3.5 cm wide, membranous, the apex acute to acuminate, the base cuneate, somewhat oblique, sharply serrate to double serrate, above green, sparsely villous, below lighter green, sparsely villous, hairs more dense along midvein; petioles slender, elongated, 1.5–5.0 cm long, reddish brown, sparsely hirsute. *Inflorescences* axillary, cymose, 4–6 flowered; peduncles ca. 5 mm long, reddish, glandular; bracts linear, ca. 1–5 cm long, serrulate, ciliate; pedicels slender, ca. 6 mm long, green or reddish glandular. *Flowers* showy; calyx lobes distinct to the base, subulate or lanceolate, ca. 2 cm long, ca. 1 mm wide at the base, remotely serrulate, reddish, ciliate; corolla white with purplish area ("eye"), and with purplish veins, the tube oblique in the calyx, ca. 3 cm long, with a 3 mm long spur at the base, infundibuliform, 2–3 mm in diam. at the base, ampliate above, ca. 1 cm wide, outside sparsely villous, inside glabrous; stamens included, the filaments adnate to the base of the corolla for ca. 5 mm, free part ca. 2.5 cm long, yellow and sparsely pubescent below, reddish above, glabrous, the anthers ca. 1 mm long, coherent in 2 pairs by their apices, the locules divergent, connective reddish; disc reduced to a single posterior gland; ovary villous apically, style reddish, pilose, the stigma bilobed. *Fruit* and seeds not seen.

Paradrymonia ommata is known only from a single collection from low elevation in the province of Bocas del Toro. The species is distinctive by the thin, narrow, sparsely villous leaves with serrate margins, and by the white sparsely villous corolla with the purple eye. The leaves of *P. lineata* (Morton) Wiehl. are more succulent and more finely toothed.

BOCAS DEL TORO: Quebrada Huron, rapid stream through evergreen seasonal forest, 90–120 m, *Kirkbride & Duke 437* (MO, REED, SCZ).

6. **Paradrymonia pedunculata** L. Skog, Brittonia 30: 325. 1978. TYPE: Panamá, *Dwyer 2268* (MO, holotype).

Epiphytic *herbs*; stems short, 2–5 cm long, 1 cm thick, appearing rhizomatous, but fibrous rooted, rugose, purplish or brown, strigillose toward the apex, glabrous below. *Leaves* unequal in a pair, the larger leaf in a pair elongate elliptic, 19–27 cm long, 7–11 cm wide, thin, the apex acuminate, the base decurrent into the petiole, dentate, above green, sparsely appressed pilose, below green to brownish pink, appressed pilose or strigillose along the veins; petioles 2–6 cm long, pilose; smaller leaves in a pair reduced to linear bracts, 1–2 cm long. *Inflorescences* in the axils of the uppermost leaves, the flowers several in a dense cyme atop the

peduncle; peduncles erect, elongate, 10–14 cm long, 1–2 mm in diam., reddish, nearly glabrous; bracts linear lanceolate, 1.0–1.7 cm long, reddish or green, sparsely pilose; pedicels short, 0.3–1.0 cm long, sparsely pilose. *Flowers* with the calyx lobes erect, briefly connate at the base, lanceolate, 7–9 mm long, 2 mm wide at the middle, green, glabrous, except the margin pilose, the apex acuminate, remotely serrate; corolla white, cream to rose or reddish, usually darker at the limb, reddish lines in the throat, the tube narrowly funnelform, to 2.5 cm long, the base slightly gibbous, 4 mm in diam. at the base, from a point 7 mm above abruptly broader to 9 mm in diam., outside long pilose, the inside glandular, the limb lobes spreading, semiorbicular, each ca. 4 mm long and 6 mm wide, entire; stamens included, the filaments adnate to the base of the corolla tube for 7 mm, free part ca. 7 mm long, contorted, yellow, glabrous, the anthers coherent, broadly and shortly sagittate, ca. 1 mm long and wide, darker on back, not bearded; disc reduced to a single posterior gland; ovary narrowly ovoid, 2–3 mm long, appressed pilose, the style ca. 1.4 cm long, sparsely pilose, the stigma narrowly stomatomorphic. *Capsule* ovoid, 5 mm long; seeds fusiform, ca. 0.5 mm long, longitudinally striate, dark reddish brown, attached to a white funicle.

The three collections of *Paradrymonia pedunculata* are all from near the Colombian border in the province of Darién, apparently from low elevations. Further collections may be expected as the area is explored.

The species differs from other species of *Paradrymonia* in the long pedunculate inflorescence. In other species the flowers are often congested in the leaf axils with the peduncles short or lacking.

DARIÉN: Cabecero del Río Pirre, *Bristan 1321* (MO). Cocalito near Panamá-Colombia border (Pacific side), *Dwyer 2163* (MO). Puerto Sta. Dorothea, *Dwyer 2268* (MO).

7. **Paradrymonia** species A.*

Large, coarse *herbs* or *shrubs*, usually epiphytic, but occasionally terrestrial; stems thick and succulent above, woody below, to 0.5 m long or more, to 2 cm thick, purplish brown and sericeous above, below brown to gray and glabrescent, with numerous adventitious roots. *Leaves* large, coarse, subequal, broadly elliptic to ovate, 15–35 cm long, 10–25 cm wide, fleshy to coriaceous, the apex acute to acuminate, the base cuneate to decurrent along the petiole, subentire to dentate, above dark green to dark purplish brown, glabrous, below green to purplish brown, sericeous along the prominent veins, a marginal vein present; petioles elongate, thick, flattened, 10–30 cm long, red purple, sparsely sericeous. *Inflorescences* axillary, congested, cymose, of several flowers; peduncles ca. 5 mm long, reddish, glabrous; bracts lanceolate, ca. 1 cm long, reddish brown, sparsely sericeous; pedicels slender, 1.0–1.5 mm long, elongating in fruit, reddish brown, glabrous to sparsely sericeous. *Flowers* short-lived, but large; calyx lobes narrowly to broadly lanceolate, 2–4 cm long, the lateral and the basal lobes united at the base into a nearly complete tube, ca. 1.5 cm in diam., but the upper lobe free

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* *Paradrymonia* species A = *P. macrophylla* Wiehl., Selbyana 5: 56, 1978.

from the lateral lobes and nearly concealed by them, curved around the corolla spur, all serrulate, dull purplish brown, sparsely sericeous to glabrous, glandular; corolla pinkish brown to purple, maculate, occasionally with yellow spots, slightly oblique in the calyx, the tube spurred at the base, arcuate above, ca. 4 cm long, ca. 5 mm in diam. just above the spur, widening to ca. 1.5 cm broad at the throat, outside glabrous, inside glandular pubescent, the limb bilabiate, ca. 3 cm across, the upper and the lateral lobes reflexed, rotund, ca. 1 cm long, ca. 1.5 cm wide, the basal lobe erect; stamens included, reaching almost to the corolla throat, the filaments curved, adnate to the base of the corolla tube for ca. 1 cm, ca. 3 cm long, glabrous, the anthers oblong, ca. 4 mm long, 3 mm wide, the cells parallel; disc reduced to a single, entire, glabrous gland, ca. 3 mm long; ovary glabrous, the style slightly curved, ca. 3 cm long, glandular pubescent, the stigma bilobed. *Capsule* laterally compressed, globose, to 1.2 cm long, dehiscing by 2 valves, white, glabrous; seeds fusiform or oblong, 0.5 mm long, longitudinally striate, dark reddish brown, attached to a fleshy white funiculus.

Upon seeing this species in the wild, it is hard to imagine it being a member of the Gesneriaceae, because of its large leaf size and coarse habit. The plants are often deep purplish colored and succulent, epiphytic on trees or terrestrial on banks. Collections of this species have been made from the provinces of Coclé and Veraguas at 500–1,100 m elevation in wet forest, and it also occurs in Colombia. Its closest relative appears to be *Paradrymonia* sp. B, which differs in having yellow corollas, narrower leaves, and smaller habit.

COCLÉ: N of El Valle de Antón, La Mesa, 1000 m, *Allen 2794* (MO, US). Cerro Pajita, hills N of El Valle, 1100 m, *Allen 3778* (MO). La Mesa above El Valle de Antón, 900–930 m, *Croat 37442* (MO). La Mesa above El Valle, *Dwyer 11886* (MO). Rivera sawmill, Alto Calvario, *Folsom 3234* (MO). La Mesa 4 km N of El Valle, 875 m, *Nee & Hale 9669* (MO). El Petroso, 7 km beyond El Copé, 800 m, *Skog et al. 4191* (MO, P, US). VERAGUAS: Between Alto Piedra School and Río Calovébora 1.8 mi beyond school, 500 m, *Croat & Folsom 34118* (MO). 15–20 km NW of Santa Fé between Escuela Agricola Alto Piedra and continental divide, 650–800 m, *Dressler 4741* (PMA). Caribbean slope above Río Primero Brazo 5 mi NW of Santa Fé, 700–1200 m, *Liesner 998* (MO).

8. **Paradrymonia** sp. B.*

Large coarse *herbs*; stems short, almost acaulescent, succulent, ca. 1 cm or more thick, the internodes short, reddish, sparsely strigillose, numerous adventitious roots at the nodes. *Leaves* appearing to be in clumps, elongate, nearly equal in a pair (?), narrowly elliptic to oblanceolate, 15–45 cm long, 6–18 cm wide, fleshy to subcoriaceous, the apex acuminate, the base attenuate, decurrent into the petiole, entire to remotely dentate, above dark green to purplish, glabrous, below green to reddish purple, sparsely strigillose along the prominent veins, lacking obvious marginal vein; petiole elongate, 10–25 cm long, thick, ca. 5–7 mm across, green to dark reddish brown, glabrescent. *Inflorescences* axillary, congested, cymes of numerous flowers; peduncles short or lacking; bracts lanceolate, ca. 1 cm long, reddish, sparsely strigillose; pedicels often elongate, 1.5–5.0

* *Paradrymonia* species B = *P. flava* Wiehl., Selbyana 5: 51, 1978.

cm long in flower, to 7 cm long in fruit, green to reddish, strigillose. *Flowers* showy; calyx lobes distinct nearly to the base, the lateral and the basal lobes nearly equal, erect, lanceolate, ca. 2.5 cm long, 2–5 mm wide at the base, the apex attenuate, the margin remotely serrulate, reddish, sparsely strigillose, the apical lobe similar, but slightly shorter and curved around the corolla spur; corolla light yellow, occasionally with golden-brown faint spots, especially on the limb, the tube spurred at the base, infundibuliform, ca. 3.5 cm long, ca. 2–3 mm in diam. above the spur, ampliate above, to ca. 8 mm in diam. at the throat, the outside sparsely strigillose, the inside glandular, the limb subbilabiate, the lobes ca. 1 cm long and wide, pilose; stamens included; filaments ca. 2.5 cm long, pubescent, the anthers oblong, 2 mm long, not bearded; disc reduced to a single posterior gland; ovary nearly glabrous, ovoid, the style reddish, densely glandular pubescent, the stigma bilobed to broadly stomatomorphic. *Capsule* 2-valved, ovoid, 1 cm long, ca. 8 mm wide, glabrescent; seeds fusiform, ca. 1 mm long, striate, dark reddish brown, the base attached to white funiculus.

This species has been collected from the provinces of Colón, Darién, Panamá and Veraguas, at low elevations in wet forests. The yellow corollas make a striking contrast with the purplish leaves.

COLÓN: Río Guanche ca. 3–5 km above bridge on Portobelo Road, 50–200 m, *Croat 36962* (MO). Lower Río Guanche, *Dressler* (PMA). Río Guanche, 1–4 km upstream from Portobelo Road, 0–100 m, *Gentry 8814* (MO). DARIÉN: Headwater of Río Tuquesa ca. 2 km air distance from continental divide, *Croat 27164* (MO). PANAMÁ: 19 km N of El Llano, *Dressler 4278* (PMA). El Llano-Cartí Road, 17.5 km from Panamerican Highway, 350 m, *Mori et al. 4608* (MO, US). VERAGUAS: 11 km from Escuela Agricola Alto de Piedra along Río Dos Bocas, Atlantic slope, *Mori & Kallunki 3153* (MO). NW of Santa Fé 11 km from Escuela Agricola Alto de Piedra in valley of Río Dos Bocas, Atlantic slope, 450–550 m, *Mori et al. 3838* (MO).

23. PHINAEA

Phinaea Benth. in Benth. & Hook. f., Gen. Pl. 2: 997. 1876. TYPE: *P. albolineata* (Hook. f.) Benth. ex Hemsl.

Perennial, terrestrial *herbs* from scaly rhizomes; stems short, erect. *Leaves* opposite, often congested at the apex of the stem; blades membranous, soft, the margins crenate, dentate, or serrate; petioles short to long. *Inflorescences* axillary, of single or many clustered flowers; pedicels slender; floral tube turbinate; calyx campanulate with 5 spreading equal or subequal lobes; corolla subrotate or cup-shaped with a short tube, the limb of 5 spreading or erect broad, subequal lobes; stamens 4, adnate to the base of the corolla tube with a short staminode, the filaments slender, exceeding the length of the anthers, the latter obovate to subglobose, the cells distinct and not confluent, dehiscent by a short slit; disc lacking, the ovary ½-inferior, the style curved, a little longer than the stamens, the stigma stomatomorphic. *Fruit* a 2-valved capsule; seeds numerous. *Chromosomes* $n = 13$ (Lee & Grear, 1963) or $2n = \pm 26$ (Lee, 1966b).

This poorly-known genus has about 6 species from México to northern South America. Two species are found in western Panamá.

The generic name, *Phinaea*, is an anagram of the name of the closely related genus, *Niphaea* Lindley.

a. Leaves deeply toothed, coarsely biserrate to lacerate; plants 7.5–22.0 cm tall; calyx lobes entire to serrulate ..... 2. *P. lacerata*
aa. Leaves crenate dentate; plants to 3 cm tall; calyx lobes serrate ..... 1. *P. albiflora*

1. **Phinaea albiflora** Rusby, Descr. New Sp. So. Amer. Pl. 124. 1920. TYPE: In glens and on ridges on the Sierra Onaca, Colombia, *Smith 2506* (US, isotype).

Low *herbs*; stems arising from scaly rhizomes, to 3 cm tall, slender, 1–3 mm in diam., reddish, pilose; unbranched. *Leaves* unequal in a pair, ovate or elliptic, 1.5–5.1 cm long, 0.9–2.8 cm wide, thin and membranous, the apex acute to obtuse, the base oblique cuneate, crenate dentate with obtuse teeth, above dark green with purple veins, pilose, below purplish with lighter prominent veins, sparsely pilose, except trichomes more dense along the veins; petioles 1–10 mm long, sparsely pilose. *Inflorescences* in upper axils, 1–2 flowers per axil; peduncles and bracts lacking; pedicels slender, 1–3 cm long, reddish, pilose. *Flowers* small; floral tube obconic, reddish, pilose; calyx lobes spreading, briefly connate at the base, the lobes unequal, with 3 longer and 2 smaller, lanceolate, 3–4 mm long, 1–2 mm wide; green with reddish veins, both sides sparsely pilose, obtusely serrate; corollas white with a pink base, nearly actinomorphic, broadly campanulate, spreading, the tube short, ca. 1 mm long, the base 1–2 mm wide, the apex of the limb 1.0–1.5 cm across, the lobes oblong, obtuse, the basal lobe ca. 4 mm long, 2–3 mm wide, the other lobes smaller, entire, slightly curved inwardly, the outside glabrous, glandular inside as well as at the margin; stamens shorter than the corolla, 4 or 5, the filaments adnate to the base of the corolla tube, curved, ca. 2 mm long, yellow, glabrous, the anthers broadly but shortly sagittate, ca. 1 mm long, 2 mm wide, yellow on back; disc lacking; ovary half-inferior, the apex pilose, the style curved, ca. 3 mm long, glabrous, the stigma stomatomorphic to capitate. *Fruit* and seed not seen.

The Panamá plants described here from Cerro Colorado in Chiriquí Province are identified with *Phinaea albiflora* from Colombia, although they differ in being slightly smaller than those of the type collection. Some of the other collections of this species from Colombia match the Panamá plants more closely than the type.

Phinaea albiflora differs from *P. lacerata* in that the latter species is a much taller plant, to 22 cm tall, the calyx lobes are at most serrulate, but usually entire, and the leaves are obviously toothed.

CHIRIQUÍ: Ridge road at Cerro Colorado, 4.3 km from main road, along stream, 1450–1750 m, *Folsom et al. 4803* (MO, US).

2. **Phinaea lacerata** Morton, Ann. Missouri Bot. Gard. 24: 203. 1937. TYPE: Panamá, *Seibert 316* (MO, holotype; US, isotype).—FIG. 30.

Slender *herbs*; stems 7.5–22.0 cm tall, seldom more than 2 mm in diam., red or green, substrigose, unbranched. *Leaves* opposite; blades lanceolate, elliptic to obovate, 2.7–13.2 cm long, 1.4–4.3 cm wide, the apex acute or acuminate, the base often oblique, acute, coarsely biserrate to lacerate, above dark green, sparsely pilose near the apex, denser toward the base, below lighter green, whitish pubes-

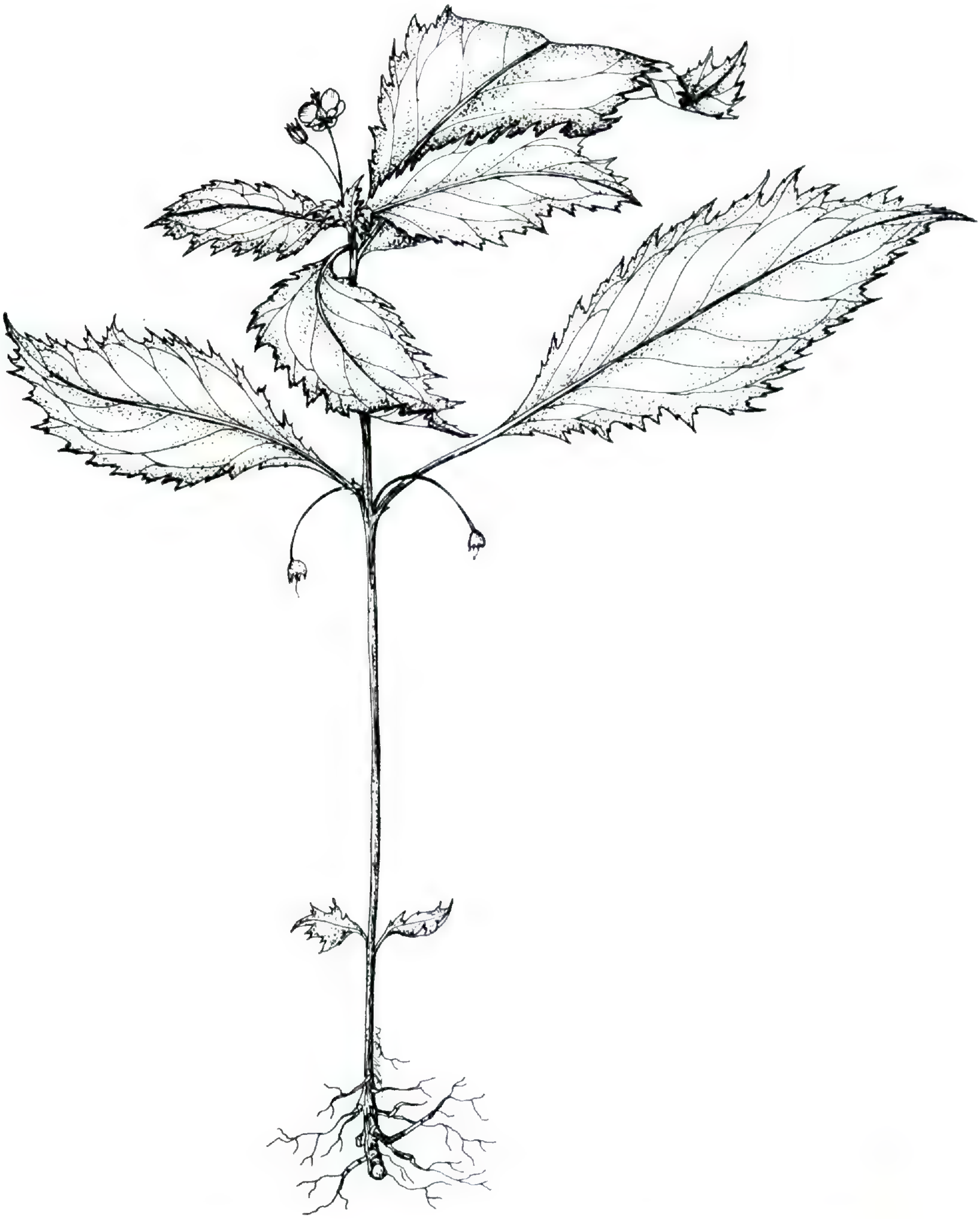

FIGURE 30. *Phinaea lacerata* Morton. Habit (×7/10). [After *White & White* 29 (US).]

cent along the veins, the veins occasionally purplish; petioles often elongate, 0.6–2.4 cm long, ca. 1 mm wide, densely pilose. *Inflorescences* of solitary subactinomorphic flowers; peduncles lacking; bracts leaflike at the base of the pedicel, ca. 3 mm long; pedicels filiform, 1.0–2.7 cm long, pubescent; floral tube turbinate, 1–2 mm long, pilose; calyx lobes lanceolate, 2–4 mm long, ca. 1 mm wide, acute, entire to serrulate, pilose and glandular resinous; corolla pink to white or cream, rotate, 11–15 mm across, the tube ca. 2 mm long, the lobes oblong, 3–5 mm long,

rounded, sparsely pilose; filaments ca. 2 mm long, curved, the anthers orbiculate, yellow, 1 mm long; disc none; ovary half-inferior, the apex glabrous, globose, the style glabrous, curved, 5 mm long. *Capsule* surrounded by the persistent calyx, globose; seeds oblong, dark brown, striate.

Phinaea lacerata is uncommon but has been found in Costa Rica and in the provinces of Chiriquí and Veraguas in Panamá. Plants inhabit damp cliffs or shaded banks at from 500–2,000 m elevation.

CHIRIQUÍ: Wet ravine W of Cerro Pando, 6000 ft, *D'Arcy & D'Arcy 6641* (MO, US). N side of Cerro Pando, 6000 ft, *D'Arcy & D'Arcy 6656* (MO). Cerro Colorado, 50 km N of San Félix, 750–800 m, *Dressler 5132* (PMA). Camp Hornitos (Fortuna dam site), 82°10'W, 8°44'N, 1000 m, *Dressler 5437* (PMA). Valley of the upper Río Chiriquí Viejo, Monte Lirio, 1300–1600 m, *Seibert 316* (MO, US). Valley of the upper Río Chiriquí Viejo, 1300–1900 m, *White & White 29* (MO, US). VERAGUAS: Guabal (Río Dos Bocas), 16 km NW of Santa Fé, 500 m, *Dressler 4795* (PMA).

24. RELDIA

Reldia Wiehl., Selbyana 2: 124. 1977. TYPE: *R. alternifolia* Wiehl.

Terrestrial *herbs*; stems perennial, erect, short, the internodes short, pubescent. *Leaves* alternate, arranged spirally, mainly clustered at the stem apex, oblanceolate to obovate, membranous or succulent, green, stomata in groups; petioles often short. *Inflorescences* in the upper leaf axils; either peduncles or pedicels elongated, pubescent; bracts lacking. *Flowers* small; calyx lobes 5, triangular to ovate, pubescent; corolla mainly white with yellow inside the tube and/or reddish spots, the tube spurred at the base, oblique in the calyx, funnelform, zygomorphic, the limb broad; stamens 4, included with an infertile dorsal staminode, the anthers dehiscing by longitudinal slits; disc reduced to a shallow or deeply bilobed posterior gland; ovary superior, pubescent, the stigma stomatomorphic. *Fruit* a dry, bivalved capsule surrounded by the persistent calyx; seeds broadly fusiform, numerous, striate.

Reldia is known only from Panamá, and it includes 2 species. The genus differs from others of the Gesneriaceae in Panamá in having alternate, spirally arranged leaves, a rare phenomenon in the family but known also in the tribe Gesnerieae (Skog, 1976) from the West Indies. It resembles *Napeanthus* in habit, occurring nearby, but that genus can be distinguished by its actinomorphic flowers.

The genus was named for Robert L. Dressler (born 1927), a noted student of Orchidaceae and pollination biology, who has lived and worked in Panamá for several years, and has an active interest in the Gesneriaceae.

a. Peduncles lacking, pedicels ca. 4 cm long; leaves obtuse; corolla to 2 cm long ..... 1. *R. alternifolia*

aa. Peduncles ca. 4 cm long, pedicels 2–5 mm long; leaves acute; corolla less than 1 cm long ..... 2. *R. veraguensis*

1. **Reldia alternifolia** Wiehl., Selbyana 2: 124. 1977. TYPE: El Llano-Cartí highway, ca. 17 km N of El Llano, Prov. Panamá, Panamá, *Dressler 4540* (SEL, holotype, not available for study; PMA, PMA, isotypes).—FIG. 31.

Terrestrial *herbs*; stems erect, to 2 dm tall, 4–5 mm in diam., with the nodes

FIGURE 31. *Reldia alternifolia* Wiehl. Habit (×7/10). [After *Skog et al. 4189* (MO).]

slightly thicker, green to reddish, the internodes to 2 cm long, shorter above and pilose, below brown, glabrescent. *Leaves* often clustered toward the stem apex; blades obovate, 6–15 cm long, 3–6 cm wide, succulent to subcoriaceous, the apex rounded or obtuse, the base cuneate, slightly oblique, remotely serrulate to crenate or nearly entire, above dark green, glabrous, below lighter green, the veins prominent, sometimes reddish, sericeous; petioles 0.5–2 cm long, green or reddish, pilose. *Inflorescences* arising from the base of the petiole, many flowers in each cluster; peduncles and bracts lacking; pedicels slender, 3–4 cm long, reddish, hirsute with reddish trichomes. *Flowers* with the calyx lobes free nearly to the base, lanceolate, elliptic or ovate, 4–6 mm long, 2–3 mm wide, the apex acute, entire, the outside pilose, the inside glabrous, the veins parallel, obvious; corolla pinkish

white with yellow lines in the tube or white with a brown lined yellow throat, and with a brownish spot at the base of each upper lobe, the tube with a broad spur at the base, oblique in the calyx, funnelform, 1.5–2.1 cm long, 2–3 mm wide at the base, 5–8 mm wide at the throat, the outside pilose above, glabrous below, the inside pubescent, the limb subbilabiate, ca. 1.3 cm across, the lobes unequal with the upper lobes shorter, ca. 5 mm long, reflexed, the lateral and basal lobes spreading, ca. 7 mm long, entire, glandular; stamens included, filaments ca. 1 cm long, curved, adnate to the base of the corolla tube for 1–2 mm, white, glabrous, the anthers coherent in 2 groups, staminode posterior, 1–2 mm long; disc reduced to a bilobed posterior gland, with minute lobes at the sides; ovary ovoid, laterally compressed, ca. 3 mm long, pilose, the style 7–8 mm long, pubescent, stigma stomatomorphic. *Capsule* globose but compressed laterally, surrounded by the persistent calyx, ca. 5 mm in diam., bivalved; seeds broadly fusiform, ca. 0.5 mm long, obliquely striate, dark reddish brown.

This species is rare in the provinces of Colón and Panamá and only represented by a few collections. *Reldia alternifolia*, where it has been found, occupies damp shady banks at about 400 m elevation.

COLÓN: Old logging road above Río Iguanita, dense second growth forest to 390 m, *Skog et al. 4189* (E, MO, US). PANAMÁ: El Llano-Cartí highway, ca. 17 km N of El Llano, wet forest near stream 400–450 m, *Dressler 4540* (PMA, PMA).

2. **Reldia veraguensis** Wiehl., Selbyana 2: 127. 1977. TYPE: Between third branch of Río Santa María and continental divide, 13–14 km NW of Santa Fé, Prov. Veraguas, Panamá, *Dressler 4831* (SEL, holotype, not available for study).

Terrestrial *herbs*; stems erect, to 10 cm long, ca. 3–5 mm in diam., but the nodes a little thicker; internodes ca. 5 mm or less long, green or reddish, the apex densely pilose, glabrescent below. *Leaves* alternate, clustered toward the apex, oblanceolate, 5–14 cm long, 2.0–4.5 cm wide, membranous, the apex acute, the base cuneate, serrulate or denticulate, especially toward the apex, ciliate, above dark green, glabrous, or rarely sparsely hirsute on the midvein, below lighter green, sparsely pilose along the veins; petioles 5–8 mm long, densely pilose. *Inflorescences* in the upper leaf axils, cymose; bracts lacking; peduncles few, slender, ca. 4 cm long, green, pilose to sericeous, the pedicels 4–6 mm long, green, pilose. *Flowers* small; calyx lobes free nearly to the base, lanceolate ovate, 3–4 mm long, ca. 1 mm wide, green, sparsely pilose, the veins parallel, prominent, the apex acuminate, entire; corolla yellow or white and yellow inside, the tube spurred at the base, oblique in the calyx, funnelform, ca. 5–8 mm long, sparsely pilose, the limb bilabiate, the lobes erect, 1–3 mm long, entire, glandular, the lateral and the basal lobes longer; stamens included, the filaments curved, the anthers divergent, ca. 0.5 mm long, coherent in 2 groups; disc reduced to a prominently bilobed posterior gland; ovary reddish, pilose, style ca. 3.5 mm long, sparsely pilose, the stigma stomatomorphic. *Capsule* globose, but laterally compressed, 2–3 mm long, bivalved, surrounded by the persistent calyx; seeds fusiform, ca. 0.5 mm long, obliquely striate, tawny.

Only two collections of this rare species have been seen—one each from the provinces of Bocas del Toro and Coclé. The specimen from Bocas del Toro, *Carleton 208* (US), differs from the description of the type, collected in Veraguas province, only in having longer leaves and a more pubescent style.

BOCAS DEL TORO: Without other locality, *Carleton 208* (US). COCLÉ: Forest around Rivera's sawmill, Alto Calvario, 7 km N of El Copé, 700–900 m, *Folsom 3215* (MO).

25. RUFODORSIA

Rufodorsia Wiehl., Selbyana 1: 139. 1975. TYPE: *R. major* Wiehl.

Epiphytic *herbs* or *subshrubs*; stems erect, ascending or decumbent, with few branches. *Leaves* opposite and decussate, nearly equal in a pair, lanceolate to ovate, membranous or succulent to subcoriaceous, toothed, pubescent; petiolate. *Inflorescences* axillary, of few to several flowers in a dense cyme; peduncles and pedicels short, bracteate. *Flowers* inconspicuous; calyx lobes 5, not all equal; corolla usually white with reddish upper side of tube and lobes, short, infundibuliform, the limb 5-lobed, somewhat bilabiate; stamens 4, not exserted, the filaments adnate to the base of the corolla tube, the anthers coherent in 2 pairs by their apices; disc of a bilobed posterior gland; ovary superior, the stigma stomatomorphic. *Fruit* a white berry; seeds with a fleshy funiculus, striate. *Chromosomes* $n = 9$ (Wiehler, 1975).

The generic name was derived from the Latin, *rufus* and *dorsum*, referring to the reddish upper lobes of the corolla. The corollas resemble those of *Koellikeria erinoides*, suggesting a similar pollinator.

Three species are included in *Rufodorsia* and all are from Costa Rica and Panamá. Often pairs of species occur in the same locality in cloud forests, but interspecific hybrids have not yet been reported, but can be expected.

Literature:

Wiehler, H. 1975. *Rufodorsia*, a new Central-American genus in the Gesneriaceae. Selbyana 1: 138–149.

a. Plants large and coarse, to 60 cm tall; leaves usually reddish on lower side, subcoriaceous, sparsely strigillose, but appearing smooth ..... 2. *R. major*
aa. Plants shorter and more slender, rarely to 50 cm tall; leaves rarely reddish on lower side, membranous but appearing thick by dense nearly sericeous hairs.
  b. Corolla limb less than 5 mm wide; calyx lobes unequal, the lower lobe larger ..... 3. *R. minor*
  bb. Corolla limb ca. 10 mm wide; calyx lobes nearly equal ..... 1. *R. intermedia*

1. **Rufodorsia intermedia** Wiehl., Selbyana 1: 144. 1975. TYPE: Panamá, *Wiehler & Dressler 71249* (US, holotype; MO, isotype).

Epiphytic, clump-forming *herbs* or *subshrubs*; stems erect or ascending, to 45 cm tall, usually shorter, woody toward the base, the internodes green or reddish, strigose. *Leaves* subequal in a pair, thick from dense, large-based hairs, elliptic to ovate, 3.5–7.0 cm long, 1.5–3.0 cm wide, the apex acute to obtuse, the base acute to

cuneate, serrate or serrulate, dark or medium green above, nearly sericeous, lighter below, green or rarely reddish and strigose pilose; petioles to 2 cm long, strigose. *Inflorescences* in the upper axils, cymose, congested and few-flowered; peduncles short or lacking; bracts lanceolate to ovate; pedicels short. *Flowers* inconspicuous; calyx lobes distinct, nearly equal, lanceolate, green, sericeous outside, nearly glabrous inside, 6–9 mm long, ca. 2 mm wide, serrulate; corolla white or cream, the upper side of the tube and the upper lobes of the limb pink, red, or orange, red spotted in throat, the tube oblique in the calyx, narrowly campanulate to funnelform, with a short rounded spur, 8–10 mm long, outside sericeous toward the limb, inside glandular pubescent in the throat, the limb spreading, ca. 1 mm wide, bilabiate with the lower and the lateral lobes rotund, ca. 3 mm long and wide, the upper lobes slightly smaller, entire; stamens included, the filaments adnate for ca. 2 mm to the base of the corolla tube, curved ca. 4 mm long, reddish, glandular pubescent, the anthers coherent in 2 pairs; disc reduced to a bilobed gland, white, glabrous; ovary pilose, the stigma stomatomorphic. *Berry* subglobose, white, pilose; seeds oblong, striate, ca. 0.5 mm long, dark reddish brown, shiny. *Chromosomes* $n = 9$ (Wiehler, 1975).

As the species epithet implies, *Rufodorsia intermedia* appears intermediate between *R. major* and *R. minor*. Although this species occurs in some of the same localities as one or the other of these two species, no apparent hybrids have been found.

Rufodorsia intermedia is found principally in the province of Coclé near El Valle, but collections have been made in Chiriquí and Panamá, and may be expected in Veraguas Province. Its habitat is in or near cloud forests.

CHIRIQUÍ: Continental divide on Cerro Colorado, 20–28 mi from San Félix, 1200–1500 m, *Croat 33381* [*p.p.*] (MO). Camp Hornitos (Fortuna dam site), 82°10′W, 8°44′N, 1200 m, *Dressler 5357* (PMA). COCLÉ: El Valle de Antón, 1000 m, *Allen 2342, 2726* (both US); *Croat 25286* (MO); *Duke & Correa 14696* (MO), *14707* (MO). Summit 7 km N of El Copé, Alto Calvario, 700–850 m, *Folsom 4168* (MO). El Petroso, 7 km beyond El Copé, 800 m, *Skog et al. 4194, 4211* (both US). Hills N of El Valle de Antón, *Wiehler & Dressler 71249* (MO, US). PANAMÁ: Cerro Jefe, 4000 ft, *Folsom & Harp 1362* (US).

2. **Rufodorsia major** Wiehl., Selbyana 1: 140. 1975. TYPE: Panamá, *Wiehler & Dressler 71176* (US, holotype; MO, isotype).—FIG. 32.

Epiphytic or rarely terrestrial coarse *herbs* or small *shrubs*; stems erect or ascending, to 60 cm tall, to 8 mm in diam., succulent or woody in older stems, usually reddish, strigose to sericeous toward the apex, glabrous below, the nodes swollen; branches few. *Leaves* equal in a pair; blades broadly elliptic, ovate or obovate, 6–15 cm long, 2–6 cm wide, subcoriaceous or fleshy, the apex acute, the base acute to cuneate, sometimes decurrent, serrulate, above dark or light green, sparsely strigillose, nearly glabrous, below deep red or maroon, rarely light green, but the veins sometimes green; petioles 0.5–2.0 cm long, strigillose. *Inflorescences* axillary of dense cymes; peduncles short or lacking; bracts lanceolate ovate, red or green, strigose to sericeous, more dense near the serulate margin; pedicels 2–5 mm long, reddish, strigillose. *Flowers* few or several per inflorescence; calyx lobes distinct, lanceolate, serrulate, unequal, the posterior lobe larger, 8–15 mm long,

FIGURE 32. *Rufodorsia major* Wiehl. Habit (×⅜). [After *Mori & Kallunki 3089* (MO).]

4–7 mm wide, the other lobes a little smaller, green, cream colored, or flushed with red, strigillose; corolla white or yellowish with reddish spots on the lower side, the upper 2 lobes dull red or orange, the tube oblique in the calyx, spurred at the base, narrowly campanulate or funnelform, 11–14 mm long, white sericeous, inside pilose, the limb spreading, ca. 1 cm across, the lobes more or less entire, unequal, basal lobe ca. 4 mm long, 6 mm wide, the lateral and the upper lobes a

little smaller; stamens 4, filaments adnate to the base of the corolla tube for ca. 3 mm, slender, curved, ca. 4 mm long, glandular, reddish toward the anthers, the anthers oblong, coherent in 2 pairs, each ca. 0.5 mm long; disc reduced to a glabrous posterior, bilobed gland; ovary pilose, the style ca. 5 mm long, reddish, glabrous above, the stigma stomatomorphic. *Berry* globose, ca. 5 mm wide, white, pilose; seeds fusiform, less than 1 mm long, striate, dark reddish brown. *Chromosomes* $n = 9$ (Wiehler, 1975).

Plants of *Rufodorsia major* are large and robust and are striking by the reddish abaxial leaf surfaces.

PANAMÁ: La Eneida, Cerro Jefe, *Dressler 3222* (PMA). Beyond Cerro Jefe, 2100–3000 ft, *Duke & Dwyer 15058* (US). Altos de Pacora, region of Cerro Jefe, 750 m, *Kennedy et al. 3361* (US). 5–10 km NE of Altos de Pacora, 600 m, *Mori & Kallunki 3342* (MO, US). Cerro Jefe ca. 20 km N of Tocumen, 800 m, *Wiehler & Dressler 71176* (MO, US). VERAGUAS: Beyond Río Tres Brazos 9 km from Santa Fé, *Croat 25603* (MO, PMA). Valley of Río Tercero Brazo beyond Escuela Agricola Alto Piedra above Santa Fé, *Croat 27336* (MO). 15–20 km NW of Santa Fé, between Escuela Agricola Alto Piedra and continental divide, 650–800 m, *Dressler 4742* (F, MO, PMA). 6.4 km outside Santa Fé on road past agriculture school, *Folsom 2982* (MO). Traditional campsite 1 km past Agriculture School, 1000–1200 m, *Folsom & Collins 1612* (US). 11 km from Escuela Agricola Alto de Piedra, Río Dos Bocas, Atlantic slope, *Mori & Kallunki 3089* (MO). NW of Santa Fé, 11 km from Escuela Agricola Alto de Piedra, valley of Río Dos Bocas, Atlantic slope, 450–550 m, *Mori et al. 3859* (MO).

3. **Rufodorsia minor** Wiehl., Selbyana 1: 142. 1975. TYPE: Panamá, *Wiehler & Dressler 71175* (US, holotype; MO, isotype).

Epiphytic *herbs*; stems erect but becoming decumbent, to 50 cm long, green or reddish, strigillose toward the apex, glabrescent below; adventitious roots at the nodes. *Leaves* nearly equal in a pair, ovate, elliptic or oblanceolate, 1.5–4.6 cm long, 0.9–2.0 cm wide, membranous, the apex acute to rounded, the base acute to cuneate, serrulate, above medium green, sericeous with whitish hairs, below lighter green, pilose; petioles to 1.2 cm long, sericeous or pilose. *Inflorescences* axillary few-flowered condensed cymes, the peduncles 3–4 mm long, sericeous; bracts leaflike, ovate or rotund, ca. 8 mm long; pedicels ca. 2 mm long. *Flowers* inconspicuous; calyx lobes distinct, elliptic, serrulate, unequal, light green, sericeous or pilose, the posterior lobe larger, 7–9 mm long, 3–4 mm wide, the other lobes slightly smaller; corolla white or cream, the upper side of the throat and the limb reddish with reddish spots on the lower side of the throat, the tube oblique in the calyx, funnelform from a rounded spurred base, 5–7 mm long, sericeous toward the limb, the limb spreading, 3–4 mm across, oblique with the lower lobe longer, ca. 2 mm long and wide, entire, the upper and the lateral lobes slightly smaller; stamens 4, not exserted, the filaments adnate to the base of the corolla tube, curved, glandular, the anthers oblong, coherent in 2 pairs by their apices; disc reduced to a single bilobed posterior gland; ovary pilose, the style red, glabrous, the stigma stomatomorphic. *Berry* globose, ca. 5 mm in diam., white, pilose; seeds fusiform or elliptic, striate, dark reddish brown, shiny. *Chromosomes* $n = 9$ (Wiehler, 1975).

Among the species of *Rufodorsia*, *R. minor* is notable for the small size of its flowers and leaves. It appeared in cultivation in the early 1960's from an un-

known source and was thought to be a new and unusual species of *Episcia*. Although it continues in cultivation, its flowers are inconspicuous and it has little to recommend it. The species is known from Costa Rica and Panamá in the lower cloud forests.

COCLÉ: El Valle de Antón, 500–1000 m, *Allen 2069* (MO), *2193* (US); *Ebinger 1113* (F, MO, US); *Hunter & Allen 318* (MO); *Woodson & Schery 191* (MO, US). COLÓN: Santa Rita lumber road E of Colón, 20 km from Transisthmian Highway, *Dressler 4135* (MO, US). PANAMÁ: Cerro Jefe, *Dressler 4040* (PMA); *Hayden 1002* (MO); *Wiehler & Dressler 71175* (MO, US). VERAGUAS: NW of Santa Fé, 2.6 km from Escuela Agricola Alto de Piedra, *Mori & Kallunki 4755* (MO, US).

26. SINNINGIA

Sinningia Nees, Ann. Sci. Nat. (Paris), sér. 1, 6: 296. 1825. TYPE: *S. helleri* Nees.

Gesnera Mart., Nov. Gen. Sp. 3: 27. 1829, not *Gesneria* L., nor *Gesnera* Cothen. TYPE: not designated.

Tapina Mart., Nov. Gen. Sp. 3: 59. 1829. TYPE: *T. barbata* (Nees & Mart.) Mart. = *Sinningia barbata* (Nees & Mart.) Nichols.

Alagophyla Rafin., Fl. Tell. 2: 33. 1837. TYPE: *A. dasyanthes* Rafin. = *Sinningia allagophylla* (Mart.) Wiehl.

Megapleilis Rafin., Fl. Tell. 2: 57. 1837. TYPE: *M. tuberosa* Rafin. = *Sinningia* sp.

Styrosinia Rafin., Fl. Tell. 2: 95. 1837. TYPE: *S. coccinea* Rafin. = *Sinningia aggregata* (Ker-Gawl.) Wiehl.

Tulisma Rafin., Fl. Tell. 2: 98. 1837. TYPE: *T. verticillata* (Hook.) Rafin. = *Sinningia* sp.

Almana Rafin., Fl. Tell. 4: 68. 1838. TYPE: *A. hirsuta* (Lindl.) Rafin. = *Sinningia hirsuta* (Lindl.) Nichols.

Fimbrolina Rafin., Sylva Tell. 77. 1838. TYPE: *F. incarnata* (Aubl.) Rafin. = *Sinningia incarnata* (Aubl.) D. Denh.

Tapeinotes DC., Prodr. 7: 544. 1839, based on *Tapina* Mart. TYPE: *T. barbata* (Nees & Mart.) DC. = *Sinningia barbata* (Nees & Mart.) Nichols.

Gesneria section *Corytholoma* Benth., Pl. Hartw. 230. 1846. TYPE: *G. stachydifolia* Benth. = *Sinningia incarnata* (Aubl.) D. Denh.

Rechsteineria Regel, Ind. Sem. Hort. Bot. Turic. [4]. 1847. TYPE: *R. allagophylla* (Mart.) Regel = *Sinningia allagophylla* (Mart.) Wiehl.

Corytholoma (Benth.) Decne., Rev. Hort. 20 [sér. 3, 2]: 466. 1848. TYPE: *Gesneria stachydifolia* Benth. = *Sinningia incarnata* (Aubl.) D. Denh.

Dircaea Decne., Rev. Hort. 20 [sér. 3, 2]: 466. 1848. TYPE: *D. bulbosa* (Ker-Gawl.) Decne. = *Sinningia* sp.

Ligeria Decne., Rev. Hort. 20 [sér. 3, 2]: 463. 1848. TYPE: *L. speciosa* (Lodd. ex Ker-Gawl.) Decne. = *Sinningia speciosa* (Lodd. ex Ker-Gawl.) Hiern.

Dolichodeira Hanst., Linnaea 26: 171, 205. 1854. TYPE: *D. tubiflora* (Hook.) Hanst. = *Sinningia tubiflora* (Hook.) Fritsch.

Stenogastra Hanst., Linnaea 26: 171, 205. 1854. TYPE: *S. hirsuta* (Lindl.) Hanst. = *Sinningia hirsuta* (Lindl.) Nichols.

Orthanthe Lem., Ill. Hort. 3: sub *tab 81*. 1856. TYPE: *O. fyfiana* (Lem.) Lem. = *Sinningia* cultivar, possibly of hybrid origin.

Biglandularia Seem., Gard. Chron. 1868: 738. 1868, not Karsten. TYPE: *B. conspicua* Seem. = *Sinningia conspicua* (Seem.) Nichols.

Rosanowia Regel, Flora 21: 33. 1872. TYPE: *R. conspicua* (Seem.) Regel = *Sinningia conspicua* (Seem.) Nichols.

× *Gloxinera* Weathers, Gard. Chron. ser. 3, 17: 144. 1895.

Terrestrial pubescent *herbs* or *shrubs*, perennial from woody tubers, or from rhizomes; stems erect or decumbent, often unbranched. *Leaves* opposite, in whorls, or congested on short stems from the tuber, nearly equal in a pair or whorl, oblong, lanceolate, or orbicular; petioles of various length or lacking.

Inflorescences axillary with one or more flowers in umbels or cymes or appearing terminal in racemes; peduncles and pedicels short or long, bracteate; floral tube short; calyx tube campanulate, the lobes 5, triangular; corolla usually red or orange, the tube campanulate to cylindric, erect, gibbous at the base, often ventricose above, limb 5-lobed, nearly regular, but more often bilabiate; stamens 4, in 2 pairs, the filaments adnate to the base of the corolla tube, the anthers coherent, dehiscing by longitudinal slits; disc of 1–5 glands, sometimes with 2 larger and connate; ovary half-inferior to superior; style slender, the stigma stomatomorphic. *Fruit* an ovoid capsule dehiscing by 2 or 4 valves; seeds small, numerous, fusiform, shiny, striate.

Sinningia is a wide ranging genus of about 75 species. It is distributed from México south to northern Argentina and Peru, to Uruguay, with many species in Brazil. Only one species is known in Panamá, the widespread S. *incarnata*.

The best known species in the genus is *Sinningia speciosa* (Lodd. ex Ker-Gawl.) Hiern and its cultivars, known as the Florists Gloxinia. This species is second only to the African Violet (*Saintpaulia* spp.) in popularity as house plants in the Gesneriaceae, and it has been in cultivation since 1817.

For a long time, many of the species of *Sinningia* were included in *Rechsteineria* Regel. Moore (1973) transferred the cultivated species of *Rechsteineria* to *Sinningia* relying heavily on the hybridization studies of Clayberg (1968, 1970).

Nees named the genus *Sinningia* for Wilhelm Sinning (1794?–1874) the head gardener at the University of Bonn.

Literature:

Arnold, P. 1975. The Gesneriad Register: *Sinningia*. The American Gloxinia & Gesneriad Society. 67 pp. and 21 appendix pp.

Clayberg, C. D. 1967. Chromosome numbers in *Sinningia* and *Rechsteineria* (Gesneriaceae). Baileya 15: 33–35.

———. 1968. Biosystematic studies in *Sinningia* and *Rechsteineria* (Gesneriaceae). Amer. J. Bot. 55: 829–833.

———. 1970. Cytology of interspecific hybrids in *Sinningia* and *Rechsteineria* (Gesneriaceae). Can. J. Gen. Cytol. 12: 759–768.

Moore, H. E. 1954. A proposal for the conservation of the name *Rechsteineria*. Baileya 2: 24–29.

———. 1973. Comments on cultivated Gesneriaceae. Baileya 19: 35–41.

1. **Sinningia incarnata** (Aubl.) D. Denh.,[18] Baileya 19: 126. 1974.—FIG. 33.

Besleria incarnata Aubl., Hist. Pl. Guiane 2: 635; 4: *tab.* 256. 1775. TYPE: Basin of Galibi Ck., French Guiana, *Aublet* (BM, holotype, not seen).

[18] Only names used for Panamá plants have been included. For additional synonymy, see Leeuwenberg, Acta Bot. Neerl. 7: 320. 1958, and Denham, Baileya 19: 126. 1974.

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FIGURE 33. *Sinningia incarnata* (Aubl.) D. Denh. Habit with flowers (×⅘). [After *Dressler 5037* (MO).]

Gesnera warszewiczii Bouché & Hanst., Ind. Sem. Hort. Berol. 1861: App. 9. 1861. TYPES: Guatemala, *Warszewicz* (B, probably not extant); México, *Karwinski* (M, not seen).
Rechsteineria warszewiczii (Bouché & Hanst.) Kuntze, Rev. Gen. 2: 474. 1891.
Corytholoma warszewiczii (Bouché & Hanst.) Standley, Publ. Field Columbian Mus., Bot. Ser. 8: 43. 1930.
Rechsteineria incarnata (Aubl.) Leeuw., Meded. Bot. Mus. Herb. Rijks Univ. Utrecht 146: 320. 1958.
Sinningia warszewiczii (Bouché & Hanst.) H. E. Moore, Baileya 19: 40. 1973.

Herbs or somewhat suffruticose; tuber woody, to 8 cm in diam., ca. 4 cm thick; stems erect, to 1 m tall, green or reddish with reddish longitudinal lines in the internodes, villous, especially toward the apex, with patent and appressed hairs, the internodes to 10 cm long; branches numerous, but often short. *Leaves* opposite, oblong, obovate, or elliptic, 4.5–9.5 cm long, 1–4 cm wide, thickened from dense vestiture, the apex acute, the base attenuate into the petiole or acute, crenate, above green, densely villous or hirsute, with broad based trichomes, below lighter or yellowish green, more densely pubescent; petioles 1–4 cm long, villous. *Inflorescences* axillary, but appearing racemiform and terminating the stem, leafy below, the leaves reduced to bracts above; peduncles 1–5 short or lacking; bracts 2, small; pedicels ca. 1 cm long, elongating in fruit, ascending, green or reddish, villous. *Flowers* showy; calyx campanulate, green or reddish, the tube 3–4 mm long, ca. 7 mm wide, the lobes broadly triangular, erect, 4–7 mm long, 2–5 mm wide, the apex acute, pilose and glandular on both sides; corolla red or red orange outside, often yellowish within, the tube 3–4 cm long, the base gibbous, ca. 7 mm wide, then narrowing to ca. 4 mm wide, broader at the middle, before narrowing just below the limb, the outside hirsute, the inside glabrous, the limb oblique, bilabiate, the upper lobes united, erect, ca. 1 cm long and wide, the lateral and the basal lobes somewhat reflexed, ca. 2 mm long, ca. 7 mm wide; stamens nearly equalling the upper corolla lobes, the filaments curved, adnate to the base of the corolla tube, 3–4 cm long, glabrous to pubescent, the anthers coherent at the apices, 1.5–2.5 mm long; disc glands 4 or 5, with 2 posterior glands large and connate; ovary conic, pubescent, the style curved, equalling the stamens, pilose. *Capsules* ovoid, ca. 1 cm long, apex acuminate; seeds fusiform or oblong, ca. 1 mm long, light brown, striate, twisted. *Chromosomes* $n = 13$ (as *Rechsteineria warszewiczii* from cultivation; Clayberg, 1967).

Sinningia incarnata ranges from México to northern Brazil, as well as in Colombia, Venezuela and the Guianas. It is thus one of the most widespread species in the genus. In Panamá, the species can be found on dry open areas on steep slopes or limestone outcrops in the Canal Zone, and in provinces of Coclé and Panamá up to 1,000 m.

The plants from Central America, long separated as a separate species from those farther south, are nearly indistinguishable from those known as *S. incarnata*. There is variation in hair-covering, coloring of sepals and corolla over the entire range.

CANAL ZONE: Madden Dam, *Bartlett & Lasser 16809* (MICH, MO, US). Flamenco Island, *Dressler 5037* (F, MO, PMA). COCLÉ: Slopes of crater around El Valle de Antón, 1000 m, *Luteyn 1244* (DUKE, MO). PANAMÁ: Stream, bordering slopes and pastures of Río Teta E of San Carlos, *Luteyn 1577* (DUKE).

27. SOLENOPHORA

Solenophora Benth., Pl. Hartw. 68. 1840. TYPE: *S. coccinea* Benth.

Arctocalyx Fenzl, Allg. Gartenzeitung 16: 305. 1848. LECTOTYPE: *A. endlicherianus* Heller ex Fenzl = *Solenophora endlicheriana* (Heller ex Fenzl) Hanst.
Hippodamia Decne., Rev. Hort. 20 [sér. 3, 2]: 464. 1848. LECTOTYPE: *H. insignis* (Martens & Gal.) Decne. = *Solenophora insignis* (Martens & Gal.) Hanst.

Suffrutescent *herbs*, *shrubs* or weak *trees*; stems usually elongate and coarse, woody, erect, terete to subquadrangular, pith usually large, brown to gray at maturity, glabrescent; few to many branches. *Leaves* opposite, nearly equal in a pair, often large, membranous, ovate to elliptic, dentate or serrate, usually dark green and pubescent to pilose above, lighter green or reddish brown and pubescent usually along the veins beneath, the lateral veins 7–10, arching toward the apex; petioles usually elongate, occasionally as long as the blades, green to reddish brown, glabrous to pilose. *Inflorescences* numerous in the leaf axils, usually pedunculate, about ½ the length of the subtending leaf; peduncles and pedicels slender, terete, green to reddish, glabrous to pilose, bibracteate. *Flowers* zygomorphic, large and showy, solitary or few per inflorescence; floral tube surrounding the ovary, glabrous to pilose; calyx of 5 lobes connate at the base, exceeding the ovary; corolla with an elongate tube, not spurred, yellow to orange or reddish orange, glabrous to pilose, the throat ampliate, the limb of 5 lobes, often spotted, suberect, broad; stamens 4, adnate to base of the corolla tube, rarely exserted, the filaments elongate, curved, broad at the base, the anthers coherent, dehiscent by longitudinal slits, the staminode small; nectary of one bilobed gland or 2, 3, or 5 glands; ovary inferior, the apex flattened or convex, the style equalling the stamens, elongated, flattened, broader toward the apex, the stigma stomatomorphic, the ovules numerous on both sides of the placental lamellae. *Fruit* a dry capsule surrounded by the persistent calyx; seeds fusiform, dark brown, striate.

Solenophora is a genus of about fifteen species from México to Panamá. The plants may be found in damp forests at mid- or high elevations. A single species, *S. calycosa*, is known in Panamá from the province of Chiriquí.

1. **Solenophora calycosa** J. D. Smith, Bot. Gaz. (Crawfordsville) 25: 152. 1898. TYPE: Slopes of Volcán Barba, Costa Rica. *Pittier* 283 (CR).—FIG. 34.

S. *australis* Morton, Ann. Missouri Bot. Gard. 26: 311. 1939. TYPE: Panamá, *Woodson et al. 846* (US, holotype; MO, isotype).
S. *toucana* Denham & Gibson, Phytologia 23: 341. 1972. TYPE: Banks of Río Sumpul, Depto. Chalatenango, El Salvador, *Tucker 1172* (UC, holotype; F, NY, US, PH, isotypes).

Stout, suffrutescent *herbs*, *shrubs* or *trees* 1–8 m tall; stems erect, to 15 cm in diam., unbranched or if branching then branched from the base or above, subterete to subquadrangular, green to dark purple or reddish brown, Panamá plants sometimes nearly glabrous but immature branches occasionally pubescent to pilose as in Costa Rican populations, the nodes glabrous; branches to 1 cm across with thicker nodes, the internodes elongate, to ca. 10 cm or more long. *Leaves* well spaced, usually present from the branch apex down to 4 or 5 nodes below the apex,

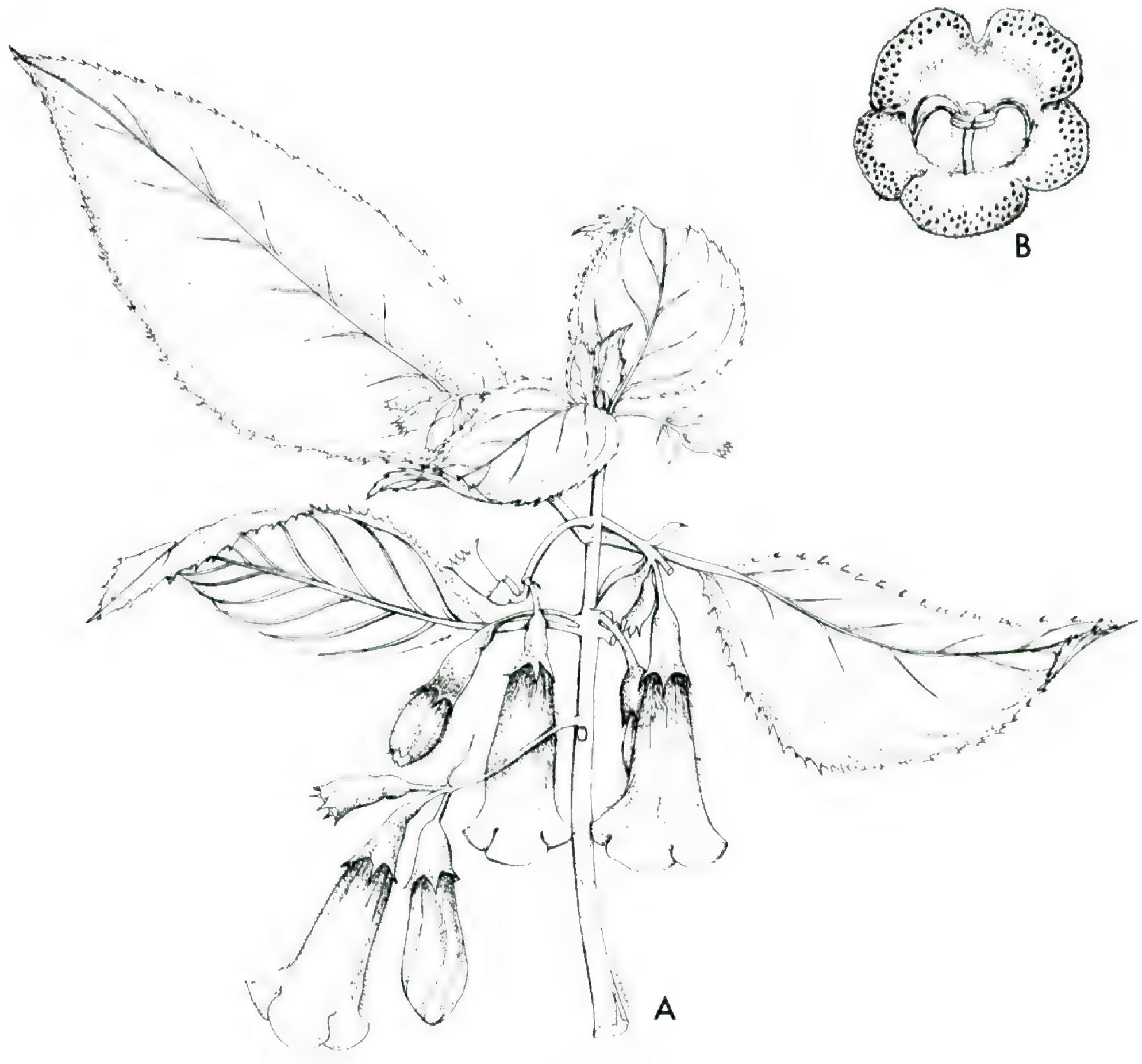

FIGURE 34. *Solenophora calycosa* J. D. Smith—A. Flowering branch (×⅖).—B. Flower (×7/10). [After *Woodson & Schery* 459 (MO).]

ovate to elliptic, 14.5–32.8 cm long, 7.1–21.3 cm wide, the apex acute or acuminate, the base often oblique, acute to cordate, biserrate, above dark green, pilose or scabrous, below light green or reddish brown to purple, sparsely pilose along the veins; petioles slender, subsulcate, those of a pair joined at the node by a band of tissue across the stem, 1.5–15.5 cm long, 2–4 mm across, green to reddish, subpilose to glabrescent below, pilose at the union with blade. *Inflorescences* erect in the leafy axils, cymose, of 1–4 flowers; peduncles solitary in each axil, often equalling the petioles, green to reddish, pilose to glabrous; bracts 2, linear, to 1.5 cm long, green, pilose; pedicels to 2.5 cm long, green or red, pilose to glabrous. *Flowers* showy; floral tube turbinate to acute, ca. 5 mm long and wide, green or reddish, pilose or glabrous, the veins prominent and extending to the tips of the calyx lobes; calyx erect, the tube 1.1–2.2 cm long, ca. 1 cm in diam., green or reddish below, often becoming reddish above, the outside often glabrous, rarely tomentose, the inside densely pilose, the lobes triangular, erect, 0.2–1.1 cm long, 0.4–0.6 cm broad at the base, green or reddish at least toward the serrate margins,

the veins prominent, the apex acute to acuminate; corolla salmon red or orange outside and orange to yellow inside, reddish to maroon or purple spots at the margin of the limb, the tube 5.5–7.0 cm long, ca. 0.8 cm broad at the base, becoming ca. 2.5 cm at the throat, outside sparsely pilose, the many-celled hairs becoming more dense toward the limb, the inside pilose at the base, above sparsely pilose with few-celled hairs to glabrous, the limb 5-lobed, subbilabiate, the lobes flaring, obovate or suborbiculate, nearly equal, 0.8–1.2 cm long, 1.2–2.2 cm wide, the margin erose, glandular pubescent or glabrescent; stamens adnate to the base of the corolla tube, the filaments connate at the base, 5–6 cm long, 1–2 mm broad at base, narrowed toward the apex, reddish, glabrous, the anthers divergent, coherent by their apices into a ring, each 2.0–4.5 mm long, 1–4 mm wide, the connective reddish, glabrous, staminode ca. 5 mm long, sterile; disc glands 2, or 1 and bilobed, posterior, pubescent; ovary apex pilose, the style 5–7 cm long, ca. 2 mm in diam., reddish, densely pilose at the base, sparsely pilose above, the stigma stomatomorphic, pubescent. *Fruit* surrounded by the accrescent floral tube and topped by the persistent calyx, globose or ovoid, ca. 1 cm in diam., green to yellow or brown, glabrescent; seeds ca. 0.5 mm long. *Chromosomes* $n = 10$ (Davidse, 1970, based on material from Costa Rica).

Solenophora calycosa was originally described from Costa Rica but is now known to occur in Guatemala, El Salvador, Honduras, as well as Panamá. Morton named a new species from Panamá as S. *australis* which he said differed from the Costa Rican plants in having glabrous or nearly glabrous ovaries, calyx tube, stems, and peduncles. Recent collections from Chiriquí show a range from nearly glabrous to pilose. The type of *Solenophora australis* is merely an example of one of the extremes, other individuals or populations from Chiriquí are as hirsute as the type of S. *calycosa* from Costa Rica.

CHIRIQUÍ: Trail from Cerro Punta to headwaters of Río Caldera, 2250–2500 m, *Allen 1450* (F, MO, NY, US). Bajo Mono-Róbalo Trail, W slopes of Cerro Horqueta, 5000–7000 ft, *Allen 4784* (MO, US). Llanos W of Gualaca, 500 ft, *Allen 5015* (MO, US). Cerro Horqueta, 7000 ft, *Blum & Dwyer 2628* (FSU, MO, SCZ). Cerro Punta, 7000 ft, *Blum et al. 2414* (MO, SCZ). Between Bambito and Cerro Punta, *Croat 10556* (MO, NY, PMA). Las Nubes, 2.7 mi NW of Río Chiriquí Viejo W of Cerro Punta, 2200 m, *Croat 22402* (MO). Top of peak between Barú and Respinga, 3000 m, *D'Arcy 10127* (MO). Just above Bajo Chorro, *D'Arcy 11100* (MO, US). Bajo Chorro, Boquete District, 6000 ft, *Davidson 39* (F, MO, US). Volcán de Chiriquí, Boquete District, 9500 ft, *Davidson 989* (F, MO). Boquete, 4500 ft, *Mrs. Davidson 9* (F). Cerro Horqueta, 5000–7000 ft, *Dwyer 8754* (MO), *Dwyer & Lallathin 8754* (NA); *Hagen & Hagen 2079* (NY); *Kirkbride 151* (F, MO, NY, SCZ). Ridge E of Cerro Horqueta, 1700–1900 m, *Luteyn & Wilbur 4604* (DUKE). Sierra Chiriquí, 4600 ft, *Maurice 859* (F, MO, US). Las Nubes 5 km NW of Cerro Punta, 6000–6500 ft, *Mori & Bolten 7253* (MO). Cerro Colorado 50 km N of San Félix on the continental divide, 1200–1500 m, *Mori & Dressler 7783* (MO, US). Quebrada El Velo near Finca Lérida, 6 km NW of Boquete, 1700 m, *Nee 10620* (MO, US). Cerro Punta, 6800 ft, *Ridgeway & Solis 2407* (MO). Cerro Punta, Florida State University Tropical Biology Station, 5500 ft, *Sawyer* (MO). Bajo Chorro near Río Caldera, 1900 m, *Skog & D'Arcy 4094A* (MO, US). Trail to Alta Respinga above town of Cerro Punta, 2500–2800 m, *Skog et al. 4011* (MO, PMA, US). Bajo Mono at Río Chiquero, 1800 m, *Skog et al. 4059* (E, MO, P, US). Lower Montane Rain Forest, Bajo Chorro, near Río Caldera, 1900 m, *Skog et al. 4067* (US). Bambito, 1 mi SW of Cerro Punta, 5600 ft, *Tyson 5643, 5648* (both FSU, MO, SCZ). 6 mi above Cerro Punta on the Boquete trail, 7500 ft, *Tyson 7157* (PMA). Bajo Chorro trail between 1 and 2.5 hrs. out of Boquete, 1600–1800 m, *Utley et al. 268* (DUKE). Río Chiriquí Viejo Valley near El Volcán, *White 229, 230* (both MO, US). Slopes approaching Cerro Horqueta 6.6 km NNE of Boquete, 1500–1800 m, *Wilbur & Luteyn 19238*

(DUKE). Ravine W of Las Nubes 5 km NW of Cerro Punta and towards Cerro Picacho, 2000–2100 m, *Wilbur & Luteyn 19359* (DUKE, MO). Trail along Bajo Chorro trail in direction of Cerro Punta, 5900–6200 m, *Wilbur et al. 17294* (DUKE, MO). Trail through Paseo de Respinga on way to Boquete, 7500 ft, *Wilbur et al. 13151* (DUKE, MICH, MO). 1 km N of Las Nubes, 2000–2300 m, *Wilbur et al. 15201* (DUKE). Casita Alta, Volcán de Chiriquí, 1500–2000 m, *Woodson et al. 846* (MO, US). Quebrada Velo, 1800 m, *Woodson & Schery 255* (MO, US). Potrero Muleto to summit, Volcán de Chiriquí, 3500–4000 m, *Woodson & Schery 459* (MO, US). Bajo Chorro, 1900 m, *Woodson & Schery 611* (MO, US).

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The previous issue of the ANNALS of the Missouri Botanical Garden, Vol. 65, No. 2, pp. 367–781 was published on 1 February 1979.

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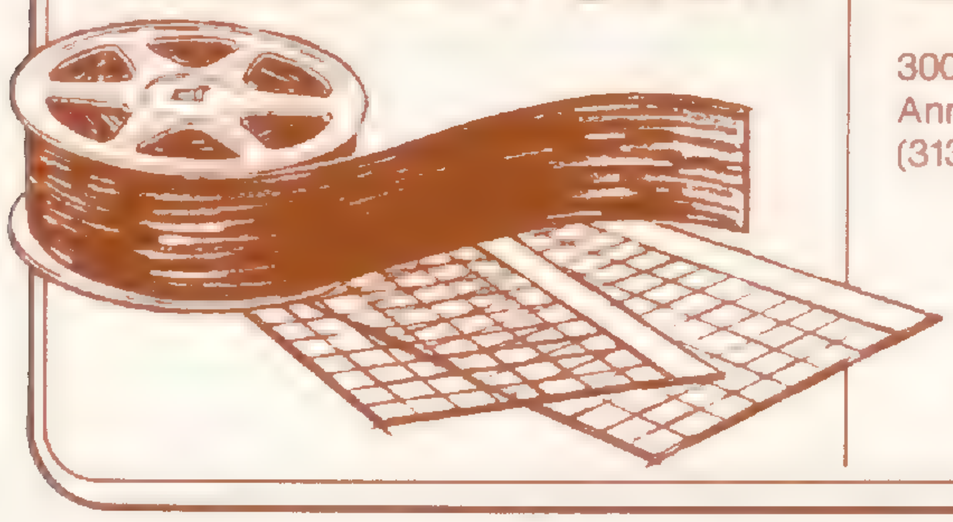

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ANNALS
OF THE
MISSOURI BOTANICAL GARDEN

VOLUME 65 1978 NUMBER 4

SYSTEMATIC ANATOMY AND PHYLOGENY OF MEXICAN COLUMNAR CACTI[1]

ARTHUR C. GIBSON[2] AND KARL E. HORAK[2]

ABSTRACT

Stem transections of 64 arborescent and fruticose species of columnar cacti were studied to evaluate present systematic treatments of Mexican taxa. Species examined included not only most Mexican taxa, primarily of tribe Pachycereeae, but also related and unrelated taxa from the West Indies and Central and South America. A review of stem biochemical literature on Mexican columnar cacti showed that triterpenes and alkaloids are mutually exclusive, except in *Lophocereus*. In taxa with abundant stem triterpenes all species of *Stenocereus* have silica bodies in the skin, whereas species of *Escontria*, *Myrtillocactus*, and *Polaskia* lack silica bodies. In species which have alkaloids, crystals are generally lacking, but in species closely related to alkaloid-bearing taxa the skin contains abundant calcium oxalate crystals in an unusual pattern. When these and other data on vegetative and reproductive morphology of Pachycereeae are used, two subtribes, Pachycereinae and Stenocereinae, can be clearly defined. Pachycereinae includes taxa that lack funicular pigment cells at anthesis but have either abundant alkaloids or calcium oxalate crystals in the skin, whereas Stenocereinae includes taxa that have abundant triterpenes and funicular pigment cells at anthesis, many which also have silica bodies. Five new combinations are proposed for Mexican species that were assigned to *Heliabravoa*, and *Machaerocereus* and *Rathbunia*, which are submerged into *Polaskia* and *Stenocereus*, respectively. Based on a proposed phylogeny of Pachycereeae, evolutionary trends of vegetative and reproductive features are analyzed. The probable center of early radiation of Pachycereeae is southern Mexico, and geographical isolation has apparently encouraged allopatric speciation of numerous phylads. The assemblage of columnar cacti in the Sonoran Desert is composed of highly specialized species of at least seven distinct phylads, and species are closely related to southern forms and not to sympatric species.

[1] Some materials for this study were collected on trips for National Science Foundation Grant GB-37664. In addition, materials were also generously contributed from the Huntington Botanical Gardens, San Marino, California; the Boyce Thompson Southwestern Arboretum, Superior, Arizona; Papago Desert Park, Tempe, Arizona; Mr. Alan Blackburn, Dr. William Heed, Mr. Lyle McGill, Dr. Thomas Starmer, Dr. Richard Wiedhof, Mr. Richard Williams, and Mr. Alan Zimmerman. The authors are indebted to Drs. William Heed, Henry Kircher, and Reid Moran for their valuable assistance in the preparation of certain sections of the manuscript and to Dr. Thomas Starmer who contributed much valuable assistance in programming the computer analysis for this study.

[2] Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona 85721.

ANN. MISSOURI BOT. GARD. 65: 999–1057. 1978.

0026-6493/78/0999–1057/$05.95/0

Nearly all species of columnar cacti have at some time been classified in the comprehensive genus *Cereus* Miller. However, since Britton & Rose (1909, 1920, 1922), who subdivided *Cereus* into numerous small genera and separated some taxa at the subtribal level, most taxonomic monographs of Cactaceae have treated *Cereus* (s. l.) as a form genus. Generic summaries by Bravo (1937), Hunt (1967), and Marshall & Bock (1941) followed the moderate generic concept of Britton and Rose with some modifications, but none expanded very much the subtribal and tribal classification of the columnar taxa. On the other hand, major liberalized classification systems (Backeberg, 1958; Buxbaum, 1958a, 1961, 1962b, 1964–1965, 1968b; Bravo, 1962–1963, after Buxbaum) emphasized the differences between species groups at the generic level and completely rearranged the columnar cacti into as many as eight tribes, all of which are ultimately derived from columnar forms in northern South America and the West Indies that appear to have the primitive features for subfamily Cactoideae. According to all of these authors, *Cereus* (s. s.) is a South American genus found east of the Andean Cordillera. The most conservative approach has been used by Benson (1969a, 1969b, 1970), but only cacti occurring in the United States were treated. Benson (1969a) recognized that *Cereus* (s. l.) is artificial but continued to use the taxon until relationships of the subdivision were better understood.

Even though investigators cannot agree on the nomenclature, classification, and phylogeny of Mexican columnar cacti, all agree that these are autochthonous species. There are about 80 species of arborescent, fruticose, suffrutescent, and procumbent forms, excluding the epiphytes but including several naturally occurring interspecific hybrids. Most species and all but three Britton and Rose genera are found only in North America. Moreover, half of the Mexican species ranging beyond Mexico extend no more than 500 kilometers beyond the border. The genus *Acanthocereus* is widely distributed along the coast of the Gulf of Mexico and occurs in the West Indies and coastal northern South America. *Cephalocereus*, a genus with numerous unresolved taxonomic problems, is wide-ranging from Mexico and Florida to Brazil; North and South American taxa are sometimes treated as separate lines or even several genera (Backeberg, 1960). Species of *Lemaireocereus* (sensu Britton and Rose) outside of Mexico occur in Central America, the West Indies, coastal Venezuela and Colombia, and the western foothills of the Andes to Peru. *Lemaireocereus griseus* (Haw.) Britt. & Rose, the only species of the genus shared between North and South America, is native to Venezuela and its adjacent islands and is probably not a native of Mexico. Patterns of very high endemism in Mexico can also be seen in subfamily Opuntioideae and in tribe Cacteae of Cactoideae. Clearly, the cactus flora of Mexico has evolved relatively independently of the cactus floras of both South America and the West Indies; therefore, Mexico is a reasonable unit for investigation as a secondary center of radiation.

In general, systematic botanists have good reasons to be suspicious of and disappointed with previous taxonomic or putatively phylogenetic treatments of columnar cacti. Gross morphological features of stems, flowers, and fruits and characteristics of growth forms and habits have proved by themselves to be

unreliable indicators of relationships within Cactoideae, in which repeated morphological convergence has occurred. Moreover, characteristics that are used to separate species and genera of cacti often appear minor, based mostly on subjective dogma of each author. Unfortunately, the absolute crossability criterion of the "biological species" is difficult to employ not only because these are long-lived perennials that may not flower for many years, but also because interspecific and intergeneric (infratribal) hybrids occur in cacti, even in nature, probably because morphological and genetic isolating mechanisms are poorly developed and pollinating agents are generally not species specific. In addition, nearly all species of columnar cacti so far analyzed are diploids, $2n = 22$ (see Leuenberger, 1976; Matuda, 1958; Pinkava et al., 1977; Pinkava & McLeod, 1971), thus ruling out the use of cytogenetic information in systematics. Systematic problems have been complicated by a plethora of specific and generic names, often proposed from insufficient materials and lacking adequate justifications for the erection of new taxa. Many of these new names have been incorporated quickly into cactus literature without much critical review. Few species have ever been studied on a population-by-population basis. Finally, systematic anatomy, which has been highly useful in unraveling the taxonomy of other families, has not been carried out with much intensity within Cactaceae.

The only current putatively phylogenetic system of classification that clearly discusses relationships of extant columnar genera is that of Buxbaum (1958a), which has undergone numerous revisions (Buxbaum, 1961, 1962b, 1968b, 1975c). According to the latest revision, tribe Pachycereeae includes nearly all large, nonepiphytic columnar cacti of Mexico, plus other species of these genera found elsewhere. Excluded from Pachycereeae are *Acanthocereus*, *Nyctocereus*, *Peniocereus*, and the epiphytic taxa, assigned by Buxbaum to Hylocereeae, and *Bergerocactus* and *Wilcoxia*, assigned to Echinocereeae. Buxbaum now has designated four subtribes, Myrtillocactinae, Pachycereinae, Pterocereinae, and Stenocereinae (once Stenocereinae and Cephalocereinae), within Pachycereeae, and he has chosen Pterocereinae, consisting of *Pterocereus* and *Escontria* of southern Mexico and Guatemala, to represent the primitive subtribe and *Stenocereus stellatus* (Pfeiff.) Riccob. to represent the primitive condition for the other derived subtribes. To date, authors have neither seriously challenged his views on primitiveness, which are the bases for the subtribes, nor carefully studied the membership of each subtribe.

Anatomical descriptions of Mexican columnar cacti are uncommon in the literature. Vegetative anatomy of a small number of unspecified species was described in the familial review of Metcalfe & Chalk (1950), and the study of Preston (1901) included the stem structure of *Carnegiea gigantea* (Engelm.) Britt. & Rose. Ergastic substances in some species have been described (Reichert, 1913; Metcalfe & Chalk, 1950). The most comprehensive study to date was done on wood anatomy (Gibson, 1973), using a comparative approach to demonstrate that quantitative and qualitative features of secondary xylem are convergent within Cactoideae, the changes being correlated with differences and similarities in growth form and habit, size, and degree of succulence. However, the classification system used was somewhat artificial for columnar forms;

therefore, comparisons between species within North America were not as convincing as between clearly unrelated species of North and South America. Numerous low magnification drawings and photographs of flowers, fruits, and seeds, either whole or in longisection, of Mexican columnar cacti have been published, but the anatomy of these structures is poorly known. Buxbaum (1962c, 1963b, 1963d, 1967, 1968b, 1969) has observed that fruit pulp color in some species of Mexican columnar cacti is produced within much enlarged, idioblastic pigment cells of the funicular epidermis, the so-called "pearl cells," whereas other species do not have this feature because the fruit matures dry, the pulp is not colored red, or the color is produced from or within the fruit wall. Buxbaum has assigned all cacti with these funicular pigment cells to tribe Pachycereeae and indicates by his phylogeny (1968b) that the character occurs in all subtribes.

Descriptions of pollen grains have been included in floristic pollen surveys (Martin & Drew, 1969, 1970) and a recent monograph on cactus pollen (Leuenberger, 1976) that reviews all cactus pollen literature. Leuenberger has concluded that most columnar cacti have a similar type of pollen grain, but for each tribe (after Buxbaum) one finds a specific range of exine features.

Because some cacti have been identified as medicinal plants, many species of Mexican columnar cacti have been biochemically investigated. Based on extensive studies of triterpenoid saponins, Djerassi (1957) was able to conclude that about 20 naturally occurring triterpenes, most of them new compounds, are present in stem tissues of columnar cacti. Especially *Escontria*, *Lemaireocereus*, *Machaerocereus*, *Myrtillocactus*, and *Lophocereus schottii* (Engelm.) Britt. & Rose have sufficient amounts of stem triterpenes to isolate and characterize the compounds. Djerassi noted that species possessing triterpenes generally lack alkaloids. Consequently, he suggested that presence of certain triterpenes may be useful in systematic studies. His suggestions and observations were used by Bravo & Cox (1958) and Buxbaum (1962c, 1963d, 1967) to argue that *Myrtillocactus*, *Polaskia*, and *Heliabravoa* are closely related, and Buxbaum (1968b, 1969) has used these data to place *Machaerocereus* into tribe Pachycereeae, which includes all species with copious amounts of triterpenes. However, no worker has yet analyzed Djerassi's findings in an attempt to clarify phyletic lines within the tribe. Moreover, taxonomists have not properly explained the systematic distribution of unusual alkaloids and steroids in some species of columnar cacti (Agurell, 1969; Agurell et al., 1971) that lack triterpenes.

Our purpose here is to report the previously unstudied anatomical diversity of the columnar cacti of Mexico, especially structures of stems, and to evaluate the similarities and differences of these structures with respect to data assembled from all sources to determine, if possible, the phyletic position of these taxa. An accurate phylogenetic picture is needed to change the nomenclature of these species. Knowledge of phyletic lines is essential for the study of the origin of physiological adaptations of cacti and to analyze the host preferences exhibited by cactophilic species of *Drosophila*, which feed on yeasts growing in rotting columnar forms.

Materials and Methods

A summary of the species examined in this study is provided at the end of this section, including authorities, approximate distributions, and, wherever available, vouchered herbarium specimens in the herbarium of the University of Arizona or Rancho Santa Ana Botanic Garden, Claremont, California. For this study the columnar cacti were defined as those species with cylindric, ribbed stems that are at least 15 times longer than they are wide. Epiphytic species were excluded because these must be studied as a unit from a wider geographic region. Moreover, adequate materials of *Morangaya*, *Neoevansia*, *Peniocereus*, and *Wilcoxia*, mostly suffrutescent forms, were not available, and a separate study should be devoted to these genera, as well as *Echinocereus* and *Bergerocactus*, to clarify phylogenetic relationships. Most Mexican species have been assigned by Buxbaum to tribe Pachycereeae, and basionyms and most commonly used synonymy are cited not only for species studied but also for other Mexican species (with asterisk).[3] Five new nomenclatural combinations are used throughout the text, where justifications are provided, to minimize confusion to the reader. Other than the epiphytic and suffrutescent forms, *Acanthocereus* and *Nyctocereus* of tribe Hylocereeae and *Bergerocactus* presumably of tribe Echinocereeae are the only other bona fide columnar cacti endemic to Mexico. Representatives of other tribes were investigated anatomically to determine whether features used in the systematics of tribe Pachycereeae occur in any unrelated columnar cacti. The reader should refer to Backeberg (1959, 1960) and Bravo (1937) for illustrations and general morphological descriptions of the columnar cacti.

Samples were obtained from mature field specimens and from cultivated plants, mostly vegetatively propagated from wild-collected plants. In most cases only one or two samples were available for study of each species.

Materials were liquid preserved in formalin-acetic acid-alcohol fixative (Johansen, 1940). Outer stem samples of ribs and valleys with spines removed were taken from healthy shoot tips just above the level of early periderm formation, so that late-developing features would not be missed. Standard paraffin methods were used to prepare microscope slides, and the thickness of sections varied with the nature of the material. Features of the hypodermis and presence of crystals and mucilage often interfered with proper embedding and sectioning. Sections were stained with safranin and fast green. Microslides were also prepared from unembedded materials of the outer stem of young and old portions to compare with embedded materials and of the vascular cylinder and pith to observe phloem sclerenchyma and pith features. Care was taken to examine fascicular regions with secondary growth because primary phloem fibers often begin to differentiate only after secondary growth has begun in cacti. Freehand sections were made to study fruit walls, but ovules, funiculi, and stamens were mounted in Hoyer's medium (Beeks, 1955), which served as a combined mounting medium and clearing agent.

This study was designed to use qualitative, rather than quantitative, anatom-

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[3] This list will be more correct when *Cephalocereus* is carefully monographed.

ical comparisons because sufficient numbers of field collections of each species could not be made to do adequate statistical analyses. In a study on cactus anatomy Conde (1975) has already shown that the dimensions of epidermal and cortical structures may be exceedingly variable within a species; however, qualitative features are relatively constant. None of the features used in this study showed marked qualitative differences for the same species between wild and cultivated specimens.

Observations on ergastic substances were made with the aid of polarized light. Starch grains were easily distinguishable, and specific microchemical tests for starch with potassium iodide-iodine (IKI, Johansen, 1940) were used only in special circumstances. Birefringent crystals were assumed to be composed of calcium oxalate or possibly calcium malate (Bailey, 1964). Microchemical tests were made of anisotropic bodies found in the collenchymatous hypodermis and epidermis of certain species to determine if they were silica bodies. Tests included immersing for 1–4 hr unstained thin sections of *Stenocereus gummosus* affixed to microslides in four different solutions: concentrated hydrochloric, nitric, and hydrofluoric acids and dilute sodium hydroxide. These bodies were tentatively identified as silica because they dissolved only in hydrofluoric acid.

Data from the literature on cactus morphology and biochemistry were combined with numerous new anatomical observations on stems and reproductive structures to construct a phylogeny that reflects the similarities and differences of Pachycereeae. Data on 69 variables were entered on computer cards for species of Pachycereeae studied, and 60 were used in the BC-TRY key-cluster analysis system (Tryon & Bailey, 1970), available in the University of Arizona computer center, to check the validity of the phylogeny devised by personal analysis. The agreement was very close in expressing the composition and positions of subtribes and smaller phylads. A list of the variables and scoring procedures is too long to be published here but will be provided to interested readers upon request.

TRIBE PACHYCEREEAE Buxb.

Backebergia militaris (Audot) Bravo ex Sánchez Mejorada.* *Cereus militaris* Audot, Rev. Hort. 2: 307. 1845. West central Mexico.

Carnegiea gigantea (Engelm.) Britt. & Rose. *Cereus giganteus* Engelm. in Emory, Notes Milit. Reconn. 159. 1848. Sonoran Desert. *Gibson* 3233 (ARIZ).

Cephalocereus alensis (Weber) Britt. & Rose. *Pilocereus alensis* Weber in Gossel., Bull. Mus. Hist. Nat. (Paris) 11: 508. 1905. Syn. *Pilosocereus alensis* (Weber) Byles & Rowl. Sinaloa to Jalisco, Mexico. *Gibson 3218* (ARIZ). May include *Pilosocereus guerreronis* (Backeb.) Byles & Rowl. of Guerrero.

Cephalocereus apicicephalium Daws.,* Allan Hancock Found. Publ. Occas. Pap. 1: 10. 1948. Syn. *Neodawsonia apicicephalium* (Daws.) Backeb. Oaxaca, Mexico.

Cephalocereus chrysacanthus (Weber) Britt. & Rose. *Pilocereus chrysacanthus* Weber in K. Schum., Gesamtb. Kakt. 1: 78. 1897. Syn. *Pilosocereus chrysacanthus* (Weber) Byles & Rowl. Southern Mexico. *Gibson 3188* (ARIZ).

Cephalocereus collinsii Britt. & Rose,* Cactaceae 4: 269. 1923. Syn. *Pilocereus collinsii* (Britt. & Rose) Knuth and *Pilosocereus collinsii* (Britt. & Rose) Byles & Rowl. Oaxaca, Mexico.

Cephalocereus cometes (Scheidweil.) Britt. & Rose.* *Cereus cometes* Scheidweil., Allg. Gartenzeitung 8: 399. 1840. Syn. *Pilocereus cometes* (Scheidweil). Knuth and *Pilosocereus cometes* (Scheidweil.) Byles & Rowl. San Luis Potosí, Mexico.

Cephalocereus gaumeri Britt. & Rose,* Cactaceae 2: 47. 1920. Syn. *Pilocereus gaumeri* (Britt.

& Rose) Knuth and *Pilosocereus gaumeri* (Britt. & Rose) Backeb. Yucatán Peninsula, Mexico.

Cephalocereus hoppenstedtii (Weber) K. Schum. *Pilocereus hoppenstedtii* Weber, Cact. Pfersdorff. 1864. Syn. *Haseltonia columna-trajani* (Karw.) Backeb. Puebla and Oaxaca, Mexico. *Gibson 2332* (RSA; dead seedling).

Cephalocereus leucocephalus (Poselg.) Britt. & Rose. *Pilocereus leucocephalus* Poselg., Allg. Gartenzeitung 21: 126. 1853. Syn. *Pilosocereus leucocephalus* (Poselg.) Byles & Rowl. Sonora to Oaxaca, Mexico. *Gibson 3206* (ARIZ).

Cephalocereus nizandensis (Bravo & MacDoug.) Buxb.* *Neodawsonia nizandensis* Bravo & MacDoug., Anales Inst. Biol. Univ. Nac. México 29: 82. 1958. Oaxaca, Mexico.

Cephalocereus nobilis (Haw.) Britt. & Rose. *Cereus nobilis* Haw., Syn. Pl. Succ. 179. 1812. Syn. *Pilosocereus nobilis* (Haw.) Byles & Rowl. Lesser Antiles. *Gibson 3207* (ARIZ).

Cephalocereus palmeri Rose,* Contr. U.S. Natl. Herb. 12: 418. 1909. Syn. *Pilocereus palmeri* (Rose) Knuth and *Pilosocereus palmeri* (Rose) Byles & Rowl. Tamaulipas and San Luis Potosí, Mexico.

Cephalocereus purpusii Britt. & Rose,* Cactaceae 2: 56. 1920. Syn. *Pilocereus purpusii* (Britt. & Rose) Knuth and *Pilosocereus purpusii* (Britt. & Rose) Byles & Rowl. Sonora to Michoacán, Mexico.

Cephalocereus royenii (L.) Britt. & Rose. *Cactus royenii* L., sp. pl., ed. 1. 467. 1753. *Pilocereus royenii* L., Illustr. Hort. 11 (Misc.): 74. 1864. Syn. *Pilosocereus royenii* (L.) Byles & Rowl. West Indies. *Heed s. n.*

Cephalocereus russelianus (Otto) Rose. *Cereus russelianus* Otto in Salm-Dyck, Cact. Hort. Dyck. 1849: 201. 1850. Syn. *Pilocereus russelianus* (Otto) Rumpl. and *Subpilocereus russelianus* (Otto) Backeb. Venezuela and Colombia. *Gibson 3228* (ARIZ). Placement of this species in *Cephalocereus* is tentative.

Cephalocereus sartorianus Rose,* Contr. U.S. Natl. Herb. 12: 419. 1909. Syn. *Pilocereus sartorianus* (Rose) Berg. and *Pilosocereus sartoranus* (Rose) Byles & Rowl. Veracruz, Mexico.

Cephalocereus senilis (Haw.) Pfeiff. *Cereus senilis* Haw., Phil. Mag. 63: 31. 1824. Syn. *Pilocereus senilis* (Haw.) Lem. Hidalgo and Guanajuato, Mexico. *Gibson s.n.* (seedling).

Cephalocereus totolapensis (Bravo & MacDoug.) Buxb. *Neodawsonia totolapensis* Bravo & MacDoug., Anales Inst. Biol. Univ. Nac. México 29: 74. 1958. Oaxaca, Mexico. *Gibson 3234* (ARIZ).

Escontria chiotilla (Weber) Rose. *Cereus chiotilla* Weber in K. Schum., Gesamtb. Kakt. 83. 1897. Puebla, Mexico, but also widely cultivated and escaped. *Gibson 2356* (RSA), *3181* (ARIZ).

Lophocereus gatesii M. E. Jones, Cact. Succ. J. 5: 546. 1934. Southern Baja California, Mexico. *McGill s. n.*

Lophocereus schottii (Engelm.) Britt. & Rose. *Cereus schottii* Engelm., Proc. Amer. Acad. Arts 3: 288. 1856. Syn. *Pilocereus schottii* (Engelm.) Lem. Sonoran Desert. *Gibson 3195* (ARIZ); *Heed s. n.*

Mitrocereus fulviceps (Weber) Backeb. ex Bravo. *Pilocereus fulviceps* Weber in K. Schum., Gesamtb. Kakt. 476. 1897. Syn. *Pachycereus chrysomallus* (Lem.) Britt. & Rose and *Pseudomitrocereus fulviceps* (Weber) Bravo & Buxb. Puebla, Mexico. *Gibson 2531* (RSA).

Myrtillocactus cochal (Orc.) Britt. & Rose. *Cereus cochal* Orc., West. Amer. Sci. 6: 29. 1889. Baja California, Mexico. *Gibson 3178* (ARIZ).

Myrtillocactus geometrizans (Mart.) Cons. *Cereus geometrizans* Mart. in Pfeiff., Enum. Cact. 90. 1837. Central Mexico from San Luis Potosí to Oaxaca. *Gibson 3176* (ARIZ).

Myrtillocactus schenckii (Purp.) Britt. & Rose. *Cereus schenckii* Purp., Monatsschr. Kakteenk. 19: 38. 1909. Puebla and Oaxaca, Mexico. *Gibson 3186* (ARIZ).

Neobuxbaumia euphorbioides (Haw.) Buxb.* *Cereus euphorbioides* Haw., Suppl. Pl. Succ. 75. 1819. Syn. *Carnegiea euphorbioides* (Haw.) Backeb., *Cephalocereus euphorbioides* (Haw.) Britt. & Rose, *Pilocereus euphorbioides* (Haw.) Rumpl., and *Rooksbya euphorbioides* (Haw.) Backeb. Veracruz and Tamaulipas, Mexico.

Neobuxbaumia macrocephala (Weber) Daws.* *Cephalocereus macrocephalus* Weber in K. Schum., Gesamtb. Kakt. 197. 1897. Syn. *Pachycereus ruficeps* (Weber) Britt. & Rose and *Pilocereus macrocephalus* Weber. Puebla, Mexico.

Neobuxbaumia mezcalaensis (Bravo) Backeb.* *Cephalocereus mezcalaensis* Bravo, Anales Inst. Biol. Univ. Nac. México 3: 379. 1932. Syn. *Pilocereus mezcalaensis* (Bravo) Marsh. Puebla, Mexico. One cannot tell from descriptions whether *N. multiareolata* (Daws.)

Bravo, Scheinv. & Sánchez Mejorada belongs in *N. mezcalaensis*. Ironically, an analysis of the genus *Neobuxbaumia* by Scheinvar & Bravo (1973), a year after *N. multiareolata* was named, did not discuss this presumed species.

Neobuxbaumia polylopha (DC.) Backeb. *Cereus polylophus* DC., Mém. Mus. Hist. Nat. 17: 115. 1828. Syn. *Cephalocereus polylophus* (DC.) Britt. & Rose and *Pilocereus polylophus* (DC.) Salm-Dyck. Hidalgo and Queretaro, Mexico. *Gibson s. n.* (young plant).

Neobuxbaumia scoparia (Poselg.) Backeb.* *Pilocereus scoparius* Poselg., Allg. Gartenzeitung 21: 216. 1853. Syn. *Cephalocereus scoparius* (Poselg.) Britt. & Rose. Veracruz and Oaxaca, Mexico.

Neobuxbaumia tetetzo (Weber) Backeb. *Pilocereus tetetzo* Weber, Hort. Paris Engelmann. 1864. Syn. *Cephalocereus tetetzo* (Weber) Bravo and *Pachycereus tetetzo* (Weber) Ochoterena. Puebla and Oaxaca, Mexico. *Gibson 3237* (ARIZ).

Pachycereus grandis Rose,* Contr. U.S. Natl. Herb. 12: 421. 1909. Central Mexico.

Pachycereus hollianus (Weber) Buxb. *Cereus hollianus* Weber in Coult., Contr. U.S. Natl. Herb. 4: 411. 1896. Syn. *Lemaireocereus hollianus* (Weber) Britt. & Rose. Puebla, Mexico. *Gibson 3198* (ARIZ).

Pachycereus marginatus (DC.) Britt. & Rose. *Cereus marginatus* DC., Mém. Mus. Hist. Nat. 17: 116. 1828. Syn. *Lemaireocereus marginatus* (DC.) Berg. and *Marginatocereus marginatus* (DC.) Backeb. Central Mexico from San Luis Potosí to Guerrero and Mexico, D. F., but also widely cultivated and escaped. *Gibson 3185* (ARIZ).

Pachycereus pecten-aboriginum (Engelm.) Britt. & Rose. *Cereus pecten-aboriginum* (Engelm.) in S. Wats., Proc. Amer. Acad. Arts 21: 429. 1886. Southern Baja California and mainland Mexico from S. Sonora to Oaxaca. *Gibson 3240* (ARIZ). Here is included *Pachycereus tehuantepecanus* MacDoug. & Bravo. The original description (Bravo, 1956b) made comparisons between the new species and *P. grandis*, which overlaps in part of its distribution, but failed to make comparisons with *P. pecten-aboriginum* with which *P. tehuantepecanus* is certainly most closely related. It appears that *P. tehuantepecanus* is a southern disjunct subspecies or race of widespread *P. pecten-aboriginum*.

Pachycereus pringlei (S. Wats.) Britt. & Rose. *Cereus pringlei* S. Wats., Proc. Amer. Acad. Arts 20: 368. 1885. Baja California and mainland Mexico from Sonora to Nayarit. *Gibson 3197, 3241, 3311* (ARIZ).

Pachycereus weberi (Coult.) Backeb. *Cereus weberi* Coult., Contr. U.S. Natl. Herb. 3: 410. 1896. Syn. *Lemaireocereus weberi* (Coult.) Britt. & Rose, *Ritterocereus weberi* (Coult.) Backeb., and *Stenocereus weberi* (Coult.) Buxb. Puebla and Oaxaca, Mexico. *Gibson 3235* (ARIZ).

Polaskia chende (Gossel.) Gibs. & Horak, comb. nov. *Cereus chende* Gossel., Bull. Mus. Hist. Nat. (Paris) 11: 506. 1905. Syn. *Heliabravoa chende* (Gossel.) Backeb. and *Lemaireocereus chende* (Gossel.) Britt. & Rose. Puebla and Oaxaca, Mexico. *Gibson 3180* (ARIZ).

Polaskia chichipe (Gossel.) Backeb. *Cereus chichipe* Gossel., Bull. Mus. Hist. Nat. (Paris) 11: 507. 1905. Syn. *Lemaireocereus chichipe* (Gossel.) Britt. & Rose. Puebla and Oaxaca, Mexico. *Gibson 3179* (ARIZ).

Pterocereus gaumeri (Britt. & Rose) MacDoug. & Miranda. *Pachycereus gaumeri* Britt. & Rose, Cactaceae 2: 71. 1920. Syn. *Anisocereus gaumeri* (Britt. & Rose) Backeb. Yucatán Peninsula and Chiapas, Mexico. *Gibson 3213* (ARIZ). Here is included *Pterocereus foetidus* MacDoug. & Miranda, which does not appear to be distinct enough to be recognized as a species separate from *P. gaumeri*. This species is provisionally treated in this tribe.

Stenocereus alamosensis (Coult.) Gibs. & Horak, comb. nov. *Cereus alamosensis* Coult., Contr. U.S. Natl. Herb. 3: 406. 1896. Syn. *Rathbunia alamosensis* (Coult.) Britt. & Rose. Sonora to Colima, Mexico west of the Sierra Madre Occidental. *Gibson 3182, 3194* ARIZ); *Horak 113*.

Stenocereus beneckei (Ehrenb.) Berg. & Buzb. *Cereus beneckei* Ehrenb., Bot. Zeit. (Berlin) 2: 835. 1844. Syn. *Hertrichocereus beneckei* (Ehrenb.) Backeb., *Lemaireocereus beneckei* (Ehrenb.) Britt. & Rose, and *Piptanthocereus beneckei* (Ehrenb.) Riccob. Guerrero and Puebla, Mexico. *Gibson 3208, 3227* (ARIZ).

Stenocereus chrysocarpus Sánchez Mejorada,* Cact. Suc. Mex. 17: 95. 1972. Michoacán, Mexico.

Stenocereus deficiens (Otto & Dietr.) Buxb. *Cereus deficiens* Otto & Dietr., Allg. Gartenzeitung 6: 28. 1838. Syn. *Lemaireocereus deficiens* (Otto & Dietr.) Britt. & Rose and *Ritterocereus deficiens* (Otto & Dietr.) Backeb. Coastal Venezuela. *Gibson 3226* (ARIZ).

Stenocereus dumortieri (Scheidweil.) Buxb. *Cereus dumortieri* Scheidweil., Hort. Belge 4:

220. 1837. Syn. *Isolatocereus dumortieri* (Scheidweil.) Backeb. and *Lemaireocereus dumortieri* (Scheidweil.) Britt. & Rose. San Luis Potosí to Oaxaca, Mexico. *Gibson 3202, 3220* (ARIZ).

Stenocereus eruca (T. S. Brandeg.) Gibs. & Horak, comb. nov. *Cereus eruca* T. S. Brandeg., Proc. Calif. Acad. Sci. 2: 163. 1889. Syn. *Lemaireocereus eruca* (T. S. Brandeg.) Britt. & Rose and *Machaerocereus eruca* (T. S. Brandeg.) Britt. & Rose. West central Baja California, Mexico. *Gibson s. n.*

Stenocereus fricii Sánchez Mejorada,* Cact. Suc. Mex. 18: 89. 1973. Jalisco to Michoacán, Mexico.

Stenocereus griseus (Haw.) Buxb.* *Cereus griseus* Haw., Syn. Pl. Succ. 182. 1812. Syn. *Cereus eburneus* Salm-Dyck, *Lemaireocereus griseus* (Haw.) Britt. & Rose, and *Ritterocereus griseus* (Haw.) Backeb. Coastal Venezuela and adjacent islands, but also naturalized throughout Mexico.

Stenocereus gummosus (Engelm.) Gibs. & Horak, comb. nov. *Cereus gummosus* Engelm., Proc. Calif. Acad. Sci. 2: 163. 1889. Syn. *Lemaireocereus gummosus* (Engelm.) Britt. & Rose and *Machaerocereus gummosus* (Engelm.) Britt. & Rose. Baja California, islands of the Gulf of California, and one region in coastal Sonora, Mexico. *Gibson 3196* (ARIZ), *s. n.* (2).

Stenocereus hystrix (Haw.) Buxb. *Cactus hystrix* Haw., Syn. Pl. Succ. 73. 1819. Syn. *Lemaireocereus hystrix* (Haw.) Britt. & Rose and *Ritterocereus hystrix* (Haw.) Backeb. Greater Antilles. *Heed s. n.*

Stenocereus kerberi (K. Schum.) Gibs. & Horak, comb. nov. *Cereus kerberi* K. Schum., Gesamtb. Kakt. 89. 1897. Syn. *Rathbunia kerberi* (K. Schum.) Britt. & Rose. Sinaloa to Michoacán, Mexico. *Gibson 3189* (ARIZ).

Stenocereus laevigatus (Salm-Dyck) Buxb.* *Cereus laevigatus* Salm-Dyck, Cact. Hort. Dyck. 1849: 204. 1850. Syn. *Lemaireocereus laevigatus* (Salm-Dyck) Borg and *Ritterocereus laevigatus* (Salm-Dyck) Backeb. Southernmost Mexico and Guatemala, assuming that the poorly known *Lemaireocereus eichlamii* Britt. & Rose of Guatemala belongs to this species.

Stenocereus longispinus (Britt. & Rose) Buxb. *Lemaireocereus longispinus* Britt. & Rose, Cactaceae 2: 89. 1920. Guatemala. *Gibson 3238* (ARIZ).

Stenocereus martinezii (G. Ort.) Buxb.* *Lemaireocereus martinezii* G. Ort., Apuntes para la Pl. Indig. de Sinaloa, Mazatlán. 1929. Sinaloa, Mexico.

Stenocereus montanus (Britt. & Rose) Buxb. *Lemaireocereus montanus* Britt. & Rose, Cactaceae 2: 97. 1920. Northwestern mainland Mexico. *Gibson 3221* (ARIZ).

Stenocereus pruinosus (Otto) Buxb. *Echinocactus pruinosus* Otto in Pfeiff., Enum. Cact. 54. 1837. Syn. *Lemaireocereus pruinosus* (Otto) Britt. & Rose. South central Mexico. *Gibson 3204, 3219* (ARIZ); *McGill s. n.*

Stenocereus queretaroensis (Weber) Buxb. *Cereus queretaroensis* Weber in Mathss., Monatsschr. Kakteenk. 1: 27. 1891. Syn. *Lemaireocereus queretaroensis* (Weber) Saff., *Pachycereus queretaroensis* (Weber) Britt. & Rose, and *Ritterocereus queretaroensis* (Weber) Backeb. Central Mexico. *Gibson 3225* (ARIZ).

Stenocereus quevedonis (G. Ort.) Buxb.* *Lemaireocereus quevedonis* G. Ort., Mexico Forest. 6: 1. 1928. Sinaloa to Michoacán, Mexico.

Stenocereus standleyi (G. Ort.) Buxb. *Lemaireocereus standleyi* G. Ort., Revista Mex. Biol. 7: 121. 1927. Syn. *Ritterocereus standleyi* (G. Ort.) Backeb. Sinaloa, Mexico. *Gibson 3217, 3331* (ARIZ).

Stenocereus stellatus (Pfeiff.) Riccob. *Cereus stellatus* Pfeiff., Allg. Gartenzeitung 4: 258. 1836. Syn. *Lemaireocereus stellatus* (Pfeiff.) Britt. & Rose. Puebla and Oaxaca, Mexico. *Gibson 2754, 3126, 3205* (ARIZ).

Stenocereus thurberi (Engelm.) Buxb. *Cereus thurberi* Engelm., Amer. J. Sci. Arts, ser. 2, 17: 234. 1854. Syn. *Lemaireocereus thurberi* (Engelm.) Britt. & Rose and *Marshallocereus thurberi* (Engelm.) Backeb. Northwestern Mexico and adjacent Arizona. *Gibson s. n.* (2).

Stenocereus treleasei (Britt. & Rose) Backeb. *Lemaireocereus treleasei* Britt. & Rose, Contr. U.S. Natl. Herb. 12: 426. 1909. Puebla and Oaxaca, Mexico. *Gibson 3191* (ARIZ).

The following are taxa for which taxonomic decisions are not finalized:

Anisocereus lepidanthus (Eichl.) Backeb. *Cereus lepidanthus* Eichl., Monatsschr. Kakteenk. 19: 177. 1909. Syn. *Escontria lepidanthus* (Eichl.) Buxb. and *Pachycereus lepidanthus* (Eichl.) Britt. & Rose. Guatemala. *Gibson 3212* (ARIZ).

Cephalocereus quadricentralis Daws.,* Allan Hancock Found. Publ. Occas. Pap. 1: 14. 1948.

Syn. *Pilosocereus quadricentralis* (Daws.) Backeb. Oaxaca and Chiapas, Mexico. No description adequately compares this species to others in southern Mexico and Central America.

Cephalocereus tehuacanus (Weing.) Borg.* *Pilocereus tehuacanus* Weing., Z. Sukkulentenk. 3: 58. 1927. Syn. *Pilosocereus tehuacanus* (Weing.) Byles & Rowl. Puebla, Mexico. Same as for *C. quadricentralis.*

Lemaireocereus thurberi (Engelm.) Britt. & Rose var. *littoralis* (K. Brandeg.) G. Linds. *Cereus thurberi* var. *littoralis* K. Brandeg., Zoe 5: 191. 1904. Syn. *L. littoralis* H. E. Gates and *Marshallocereus thurberi* var. *littoralis* Backeb. Cape region, Baja California, Mexico. *Gibson 3000* (ARIZ). This plant closely resembles *Stenocereus thurberi* but is dwarfed in most features and has very gray stems. A relationship to *S. thurberi* is clearly observed, and it is likely that *littoralis* is an interspecific hybrid between *thurberi,* which served as the female, and *S. gummosus* or *Lophocereus schottii.*

Stenocereus chacalapensis (Bravo) Bravo.* *Ritterocereus chacalapensis* Bravo, Cact. Suc. Mex. 2: 50. 1957. Narrow endemic in Oaxaca, Mexico. This species superficially resembles several species of *Stenocereus* and to a certain extent *Pachycereus hollianus* and *Backebergia militaris.* Intensive study is needed to determine to which group *S. chacalapensis* belongs or if this narrow endemic arose as an intergeneric hybrid.

TRIBE CACTEAE

Ferocactus robustus (Link & Otto) Britt. & Rose. Puebla, Mexico. *Gibson 2546* (RSA).

TRIBE CEREEAE

Cereus aethiops Haw. Argentina. *Gibson 3061* (ARIZ).
Cereus dayamii Speg. Argentina. *Gibson 2746* (RSA).
Monvillea cavendishii (Monv.) Britt. & Rose. Southern Brazil to northern Argentina. *Gibson 2757* (RSA).
Stetsonia coryne (Salm-Dyck) Britt. & Rose. Argentina. *Gibson 3056* (ARIZ).

TRIBE ECHINOCEREEAE

Bergerocactus emoryi (Engelm.) Britt. & Rose. Coastal northern Baja California and offshore islands and adjacent California. *Gibson 1970* (RSA).

TRIBE HYLOCEREEAE

Acanthocereus horridus Britt. & Rose. Southern Mexico and Guatemala. *Gibson 3184* (ARIZ).
Acanthocereus pentagonus (L.) Britt. & Rose. Coastal North America around the Gulf of Mexico, sometimes inland. *Gibson 3223* (ARIZ); *Stern 3026* (MARY).
Acanthocereus subinermis Britt. & Rose. Oaxaca, Mexico. *Gibson 3209* (ARIZ).
Harrisia martinii (Labour.) Britt. & Rose. Argentina. *Gibson 2751* (RSA).
Harrisia pomanensis (Weber) Britt. & Rose. Argentina. *Gibson 3059* (ARIZ).
Nyctocereus chontalensis Alex. Oaxaca, Mexico. *Gibson 3216* (ARIZ).
Nyctocereus serpentinus (Lagasca & Rodrig.) Britt. & Rose. Southern Mexico. *Gibson s. n.*

TRIBE LEPTOCEREEAE

Armatocereus (*Lemaireocereus*) *humilis* (Britt. & Rose) Backeb. Colombia. *Gibson 3183* (ARIZ).
Armatocereus (*Læmaireocereus*) *laetus* (H. B. K.) Backeb. Peru. *Gibson 3229* (ARIZ).
Leptocereus quadricostatus (Bello) Britt. & Rose. Puerto Rico. *Heed s. n.*
Samaipaticereus corroanus Card. Bolivia. *Gibson 3210* (ARIZ).

TRIBE TRICHOCEREEAE

Trichocereus spachianus (Lem.) Riccob. Argentina. *Gibson 2755* (RSA).
Trichocereus thelegonus (Weber) Britt. & Rose. Argentina. *Gibson 2761* (RSA).

Stem Chemistry

Table 1 is a summary from the literature of the species of Pachycereeae known to have abundant triterpenoid saponins (glycosides) in stem tissues. Listed

are all species of *Escontria*, *Myrtillocactus*, and *Polaskia* (incl. *Heliabravoa*) and most species of *Stenocereus* (incl. *Machaerocereus* and *Rathbunia*) recognized in this study except S. *deficiens* from South America, which is reported to have only traces of these compounds (Djerassi, 1957). *Stenocereus chacalapensis*, S. *chrysocarpus*, S. *fricii*, S. *laevigatus*, S. *martinezii*, and S. *standleyi* have never been examined for triterpenes, and triterpenes in the rathbunias have not been identified (Bird, 1974). *Cephalocereus senilis* and *Mitrocereus fulviceps* (*Pachycereus chrysomallus*) of Pachycereeae, *Armatocereus* (*Lemaireocereus*) *humilis* of Leptocereeae, and *Trichocereus peruvianus* Britt. & Rose of Trichocereeae also have traces of unidentified triterpenes, and *Armatocereus aragonii* (Weber) Backeb. possesses a mixture of amyrins, simple triterpenoid derivatives from squalene. *Lophocereus schottii*, which has abundant alkaloids and sterols, has a single triterpene, lupeol, but this compound is not present as a glycoside in stem tissues. Lupeol has very recently been isolated from *Stenocereus thurberi* (H. W. Kircher, pers. comm.). Other nonglycosidic triterpenes are calenduladiol, reported from *Stenocereus thurberi* (Bird, 1974), and betulin, found in S. *griseus*. Interestingly, betulin is the probable biochemical precursor of betulinic acid, which occurs in S. *hystrix*, the closest relative to S. *griseus*.

In Table 1 species are arranged so that taxa with similar sets of triterpenes are placed next to each other. Nearly all species have oleanolic acid, but in addition each group of species has one or several common triterpenes. For example, five of the first six species share chichipegenin; eight of the first ten share longispinogenin; three of the four species of *Myrtillocactus* have cochalic acid, longispinogenin, and myrtillogenic acid, the acid of the triol longispinogenin; and the Caribbean and Central American species of *Stenocereus* share erythrodiol. Queretaroic acid is apparently restricted to species of *Stenocereus*.

An analysis of the structures of cactus triterpenes shows that there are two biosynthetic groups (Table 1), those derived from β-amyrin, resulting in the oleanane series, and the lupane series. The least hydroxylated compounds of the oleanane series are erythrodiol, oleanolic aldehyde, oleanolic acid, and maniladiol, and it appears that oleanolic acid and erythrodiol have served as base triterpenes from which a diversity of compounds has arisen. For example, queretaroic, machaerinic, and cochalic acids are diols of oleanolic acid, and treleasegenic acid appears to be the triol of queretaroic acid. In the lupane series, betulinic acid is a monohydroxy acid whereas thurberogenin and stellatogenin are diol and triol lactones, respectively. Biochemists generally agree that compounds with greater numbers of hydroxyl and ester groups (lactones) are more elaborated molecules than those that lack them.

Alkaloids have been identified in relatively few Pachycereeae, in part perhaps because a number of the arborescent species likely to have these compounds have not been investigated. So far, pilocereine has been discovered in both species of *Lophocereus* (Djerassi et al., 1953; Djerassi et al., 1954; West et al., 1975) and in *Pachycereus marginatus* (Djerassi et al., 1954), and two related alkaloids, piloceredine and lophocerine, occur in *Lophocereus schottii* (Djerassi et al., 1958). Simple tyramine alkaloids occur in other species, including carnegine in *Carnegiea gigantea* and *Pachycereus pecten-aboriginum* (see Willaman

TABLE 1. Summary of triterpenes isolated from saponins (glycosides) from stems of Pachycereeae. Unless indicated by a footnote, reports are cited in Djerassi (1957).

	Oleanane Series																Lupane Series		
Taxon	Oleanolic Acid	Oleanolic Aldehyde	Erythrodiol	Maniladiol	Chichipegenin	Longispinogenin	Myrtillogenic Acid	Cochalic Acid	Hystrix Lactone	Dumortierigenin	Queretaroic Acid	Treleasegenic Acid	Machaerinic Acid	Machaeric Acid	Gummosogenin	Betulinic Acid	Thurberogenin	Stellatogenin
Polaskia chende	+[a]	+[b]	+[b]		+[a]													
P. chichipe	+				+	+												
Myrtillocactus schenckii	+																	+
M. geometrizans					+	+	+	+										
M. geometrizans f. *grandiareolatus*	+				+													
M. eichlamii Britt. & Rose	+			+	+	+	+	+										
M. cochal					+	+	+	+										
Escontria chiotilla				+		+												
Stenocereus longispinus	+	+			+													
S. *griseus*	+	+			+													
S. *hystrix*	+	+			+											+		
S. *pruinosus*	+																	
S. *dumortieri*										+								
S. *stellatus*	+															+	+	+
S. *treleasei*	+										+						+	+
S. *thurberi*	+								+[c]								+	
S. *eruca*																+		+
S. *gummosus*												+	+	+				
S. *queretaroensis*	+								+									
S. *beneckei*	+								+									
S. *montanus*	+								+									
S. *quevedonis*	+				+											+		
S. *alamosensis*	Present[d]																	

[a] In Bravo & Cox (1958).
[b] Shamma & Rosenstock (1959).
[c] H. W. Kircher (unpubl. data).
[d] Bird (1974).

& Schubert, 1961); gigantine (Hodgkins et al., 1967; Agurell, 1969), an isomer of pellotine (Brown et al., 1968), and salsolidine (Bruhn et al., 1970) in *C. gigantea*; anhalonidine in *Pachycereus weberi* (Djerassi et al., 1954); and 3-hydroxy-4-methoxyphenethylamine in *P. pecten-aboriginum* (Agurell et al., 1971). Dopa-

mine, the precursor of these alkaloids, occurs at high concentrations in *C. gigantea* (Steelink et al., 1967) and *Pachycereus hollianus* (Sánchez Mejorada, pers. comm.). An assortment of other alkaloids is known from other columnar cacti (Willaman & Schubert, 1961), but none occurs in species with abundant triterpenes.

Steelink et al. (1967) have determined that the blackening of wounded tissues in *Carnegiea gigantea* results from the successive conversion of dopamine, the most abundant nitrogenous compound, to oxidized quinone, to dopamino-chrome, and, finally, to melanin. It is interesting to observe that all six recognized species of *Pachycereus* show reddening and then blackening of wounded tissues, and three of these species have been shown to possess abundant dopaminelike alkaloids. In species with abundant triterpenes, blackening does not occur; instead, in most species with triterpenes the green ground tissues become bright red orange during drying, but the color fades when completely dry. Whether this color reaction is similar to that observed in *C. gigantea* has not been determined. At least in *Stenocereus dumortieri*, *S. pruinosus*, and *S. thurberi* the cortex is yellow when fresh, and *S. thurberi* has bright yellow inner bark. The chemical responsible for this coloration in *Stenocereus* has not been identified but may be a carotenoid because the pigment is extractable with chloroform, not with aqueous solutions (H. W. Kircher, pers. comm.).

External Shoot Morphology

Growth form and habit are particulary difficult to summarize for columnar cacti because even within a single tribe one often finds a nearly continuous series of designs from tall arborescent to procumbent species. The following is a useful but somewhat artificial classification design of Mexican Pachycereeae:[4]

I. Tall arborescent (> 7 m).
   - A. Solitary (unbranched) columnar; stems very thick with extremely wide pith—*Cephalocereus hoppenstedtii* (25), *C. senilis* (25), *C. totolapensis* (28), *Neobuxbaumia mezcalaensis* (15), and *N. polylopha* (29).
   - B. Excurrent columnar with relatively few ascending or spreading stems; stems very thick with extremely wide pith—*Carnegiea gigantea* (18; also IA), *Neobuxbaumia macrocephala* (24), and *N. tetetzo* (15).
   - C. Columnar with well-developed trunk and numerous straight, very long, ascending stems; stems thick to very thick with wide to extremely wide pith, respectively—*Backebergia militaris* (8), *Mitrocereus fulviceps* (14), *Pachycereus grandis* (10), *P. pecten-aboriginum* (11), *Stenocereus chacalapensis* (7), *S. chrysocarpus* (7), and *S. dumortieri* (6).
   - D. Large candelabra with a massive trunk and numerous very long, ascending stems arising from several main, massive branches; stems thick with wide pith—*Pachycereus weberi* (10).
   - E. Decurrent with a large trunk, having erect or spreading stems that are often branched (similar to IB and IC); stems thick with very wide pith—*Neobuxbaumia scoparia* (19) and *Pachycereus pringlei* (13).
   - F. Decurrent with prominent trunk, having erect or spreading stems that are often branched; stems moderate in thickness with moderate pith 2–4 cm diam.—*Cephalocereus leucocephalus* (12) and *Stenocereus griseus* (10).

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[4] Approximations of each growth habit are based on the largest and most typical design of a species, not on atypical varieties and forms. Mode rib number for each species is indicated in parentheses.

II. Small arborescent and large fruticose (4–7 m).
  A. Solitary columnar or with few ascending branches; stems moderate in thickness with narrow pith—*Neobuxbaumia euphorbioides* (9) and *Pachycereus hollianus* (11).
  B. Decurrent and divaricate with short trunk, forming a nearly flat-topped crown; stem moderate in thickness with pith narrow to 3 cm diam.—*Escontria chiotilla* (7), *Myrtillocactus cochal* (7), *M. geometrizans* (6), *M. schenckii* (8), *Polaskia chende* (7), and *P. chichipe* (9).
  C. Decurrent with short trunk and numerous erect or spreading stems that are long and sometimes branched (similar to IF); stems mostly moderate in thickness with varying amounts of pith development—*Cephalocereus* spp. (7–9), *Pterocereus gaumeri* (3), *Stenocereus fricii* (5), *S. laevigatus* (6), *S. pruinosus* (5), *S. queretaroensis* (7), and *S. standleyi* (4).
  D. Large fruticose with very short trunk and numerous, mostly unbranched, ascending stems (similar to IF and IIC); stems moderate to relatively thick with well-developed pith except in *S. stellatus*—*Cephalocereus* spp. (7–12), *Lophocereus schottii* (7, but very variable; see Felger & Lowe, 1967), *Stenocereus martinezii* (9), *S. montanus* (8), *S. quevedonis* (8), *S. stellatus* (10), *S. thurberi* (15), and *S. treleasei* (20).
  E. Small candelabra (as in ID); stems relatively thick with relatively wide pith—*Pachycereus marginatus* (5). Wherever cultivated, this species assumes a growth habit similar to IIA.

III. Miniature arborescent and fruticose (< 4 m).
  A. Excurrent with a few spreading stems; stems thick with wide pith—*Cephalocereus nizandensis* (25), *C. purpusii* (12).
  B. Ascending stems from a short base (similar to IID); stems moderate to somewhat slender with relatively narrow to moderate pith—*Cephalocereus apicicephalium* (23), *Lophocereus gatesii* (13).
  C. Spreading or arching stems from a common base; stems moderate to relatively slender with narrow pith—*Stenocereus alamosensis* (7), *S. beneckei* (7), *S. gummosus* (8), and *S. kerberi* (4).

IV. Procumbent—*Stenocereus eruca* (11).

Detailed descriptions and illustrations of the growth habits classifed above as well as those of other species in the study are not presented here because many readily available accounts include these data (Backeberg, 1959, 1960; Bravo, 1937; Britton & Rose, 1920; Marshall & Bock, 1941). There too the reader may find in-depth information on the features of stem areoles. One characteristic that needs to be emphasized is the presence of red-colored glandular trichomes in young areoles of *Stenocereus beneckei*, *S. chrysocarpus* (Sánchez Mejorada, 1972), *S. martinezii*, *S. montanus*, *S. queretaroensis*, *S. quevedonis*, and *S. thurberi*. Shreve & Wiggins (1964) have observed in *S. thurberi* that minute viscid droplets are exuded from these hairs that coalesce to form a waxy mass.

Anatomy of the Shoot

Origin of Ground Tissues

Ontogeny of succulence in columnar cactus stems below the shoot tip has never been described. Enlargement of the pith results from divisions in various planes of cells produced from the rib meristem, and at maturity the vacuolate, isodiametric cells are loosely packed, showing no radial or longitudinal lineages of cells. The inner cortex is formed in the same manner at the pith but from derivatives of the flanking (generative) meristematic zone (after Boke, 1941); however, the much-enlarged outer cortex, including succulence in the ribs, is produced principally by a subprotodermal meristem, the initials of which divide periclinally to produce cells in radial files. Derivatives of this meristem greatly

enlarge radially but often remain in files for several to many years. These cells sometimes divide again, mostly periclinally; but eventually cells round up with increased vacuolation, and large intercellular spaces are created. Cell divisions of cortical ground tissue then cease. If present, mucilage cells differentiate as idioblasts where divisions of pith or cortical cells are no longer observed.

SKIN

The "skin" by our definition is the tough, xeromorphic, but also flexible, covering on a cactus stem consisting of the epidermis, covered by a cuticle, and, in most Cactaceae, a collenchymatous hypodermis. In columnar cacti the epidermis and hypodermis are fully formed several millimeters from the shoot apex within the apical depression. Thereafter, major qualitative changes are usually not observed in the numerous cell layers in the skin until the first phellogen is initiated, commonly from epidermis. This regular pattern helps to standardize sampling methods.

Most cacti have a single-layered epidermis derived from a uniseriate protoderm, but many Pachycereeae have a multiple epidermis (Table 2). In one form of multiple epidermis, each epidermal cell, functioning as a mother cell, undergoes periclinal, anticlinal, and oblique divisions to produce a cluster of cells of various sizes (Fig. 1). In *Lophocereus schottii*, *Neobuxbaumia tetetzo*, *Polaskia chende*, *P. chichipe*, *Stenocereus stellatus*, and *S. treleasei*, each cluster, containing up to ten cells, is distinct and raised, forming a minutely bullate surface. Thicker deposits of cuticle clearly separate adjacent clusters (Fig. 2). *Armatocereus humilis* (Leptocereeae), *Cephalocereus russelianus*, and *Lophocereus gatesii* (Fig. 3) have similar but fewer-celled clusters; and in the latter, cells are often curiously nippled. In *Escontria*, *Myrtillocactus*, nearly half the species of *Stenocereus*, *Samaipaticereus corroanus*, and *Trichocereus thelegonus*, large epidermal cells commonly proliferate by periclinal (Fig. 4), anticlinal, and oblique divisions, forming two to several smaller daughter cells. Late-formed walls are generally thinner than original walls. Because such divisions occur after the cuticle has been deposited, the epidermal surface cannot expand and remains flat. In *Carnegiea gigantea* (Fig. 5), *Myrtillocactus cochal*, *M. geometrizans*, *Pachycereus pecten-aboriginum*, and *Stenocereus thurberi*, four species with thick skins, the epidermis is distinctly biseriate; and *Pachycereus pringlei* often has a triseriate epidermis. All the walls of these multiple epidermises have the same relative thickness, and the layers appear to be derived from separate cell layers. Developmental data are needed to determine whether multiple layers arise from original tunica layers or from layers produced by the subprotodermal meristem.

Outer periclinal epidermal walls are typically flat to slightly convex and smooth, but in some species walls are strongly convex or papillate, e.g., in *Nyctocereus chontalensis*. The two species of *Cereus* examined have irregular outer walls. In *Escontria chiotilla*, *Mitrocereus fulviceps*, *Myrtillocactus schenckii*, and *Pachycereus marginatus* (Fig. 6), the outer periclinal walls have conspicuous hornlike projections; and in *Myrtillocactus cochal*, *M. geometrizans*, and *Pachycereus hollianus*, projections are present but less prominent.

TABLE 2. Anatomical features of the skin. Species of Pachycereeae are arranged within each group so that plants with closely similar skin anatomy are placed together.

Taxon	Maximum Cuticular Thickness (μm)	Cuticular Features (see text)	Type of Multiple Epidermis (see text)	Epidermal Silica Bodies, Range of Diameters (μm)	Epidermis Prismatics: No./Cell, Maximum Length (μm)	Hypodermal Thickness, Range of Diameters (μm)	Hypodermal Silica Bodies, Range of Diameters (μm)	Hypodermal Solitary Prismatics, Maximum Length (μm)
Pachycereeae with abundant triterpenes								
Escontria chiotilla	30	horns; rough	internal divisions			395–570		
Myrtillocactus schenckii	23	horns; rough	internal divisions			680–790		
M. goemetrizans	15	horns; rough	internal divisions			395–510		
M. cochal	15	horns; rough	internal divisions			695–790		
Polaskia chichipe	1.3	smooth	bullate clusters			<50		
P. chende	2.2	smooth	bullate clusters			<30		
Stenocereus stellatus	1.1	smooth	bullate clusters			170–370	12–21	
S. treleasei	1.1	smooth	bullate clusters			130–180	9–18	
S. thurberi	2.9	smooth	multiple layers	3–12		180–395	9–24	
Lemaireocereus thurberi var. *littoralis*	3.5	smooth		3–9		70–125	6–12	
Stenocereus gummosus	2.6	smooth		9–18		190–285	12–35	
S. eruca	3.5	smooth				90–170	12–21	
S. hystrix	3.2	smooth	internal divisions	3–6		180–270		
S. longispinus	3.5	smooth	internal divisions	3–6		340–380	6–12	
S. deficiens	2.9	smooth	internal divisions	6–12		180–215		
S. pruinosus	2.9	smooth		6–15		285–340	6–12	
S. dumortieri	2.9	smooth		6–9		240–370	12–18	
S. queretaroensis	1.1	smooth	internal divisions	3–6		230–285	6–9	
S. montanus	2.1	smooth	internal divisions	6–9		190–230	3–6	
S. beneckei	2.4	smooth; epicutular wax		3–9		170–230		
S. standleyi	2.9	smooth	internal divisions	6–12		170–210	6–12	
S. kerberi	1.1	smooth		3–9		160–210	6–12	
S. alamosensis	1.5	smooth		3–9		100–170		

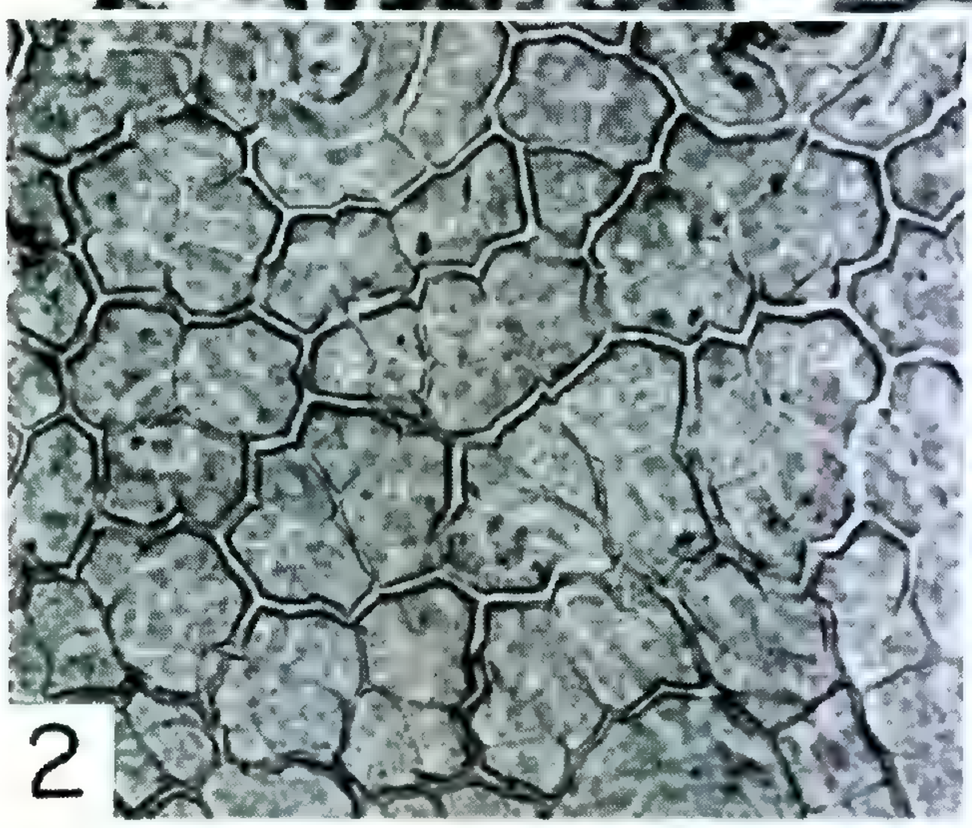
TABLE 2. Continued

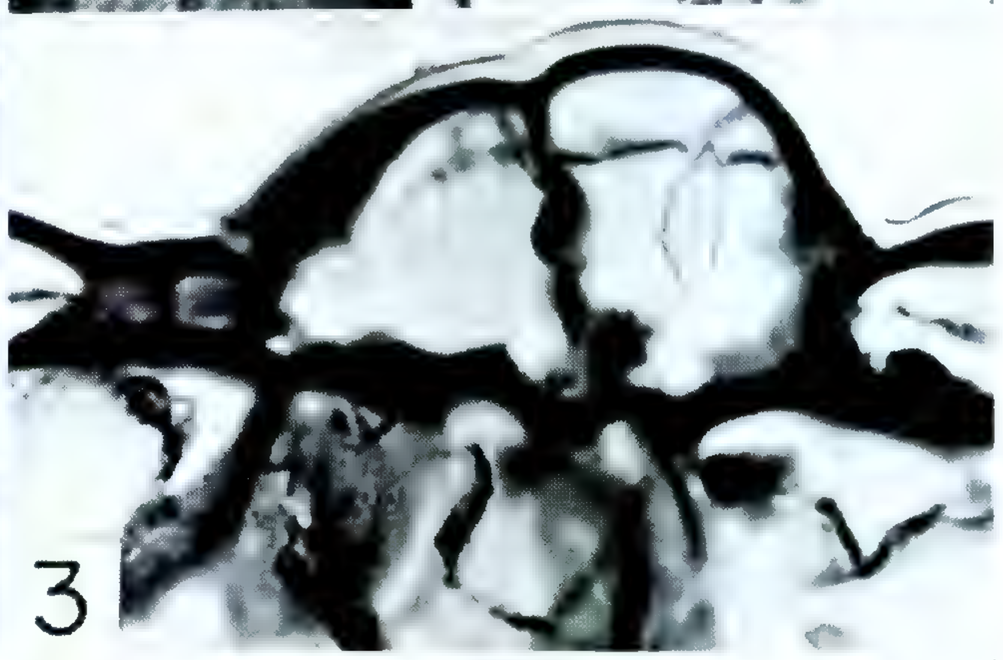
Taxon	Maximum Cuticular Thickness (μm)	Cuticular Features (see text)	Type of Multiple Epidermis (see text)	Epidermal Silica Bodies, Range of Diameters (μm)	Epidermis Prismatics: No./Cell, Maximum Length (μm)	Hypodermal Thickness, Range of Diameters (μm)	Hypodermal Silica Bodies, Range of Diameters (μm)	Hypodermal Solitary Prismatics, Maximum Length (μm)
Pachycereeae lacking abundant triterpenes or not analyzed chemically								
Pachycereus pringlei	43	wavelike ridges	multiple layers			530–860		
P. pecten-aboriginum	18	rough	multiple layers			210–250		
P. weberi	9.0	1 ridge/cell				625–730		
P. marginatus	15	horns; rough				280–340		
P. hollianus	5.8	small horns; rough				<50		
Lophocereus schottii	12	smooth; epicuticular wax	bullate clusters			90–145		
L. gatesii[a]	2.6	smooth with nipples	small bullate clusters		few, 12	50–60		
Mitrocereus fulviceps	12	reticulate ridges; horns			few, 24	600–675		125
Carnegiea gigantea	15	radiating striations	multiple layers			510–680		
Neobuxbaumia tetetzo	7.5	smooth; epicuticular wax	bullate clusters		many, 15	150–180		
N. polylopha[a]	2.6	smooth			many, 18	120–180		
Pterocereus gaumeri	3.9	smooth				90–200		
Cephalocereus russelianus	5.8	smooth	small bullate clusters			55–80		
C. totolapensis	1.3	smooth	small bullate clusters		many, 12	110–135		
C. hoppenstedtii[b]	n.a.	n.a.	n.a.		many, 30	n.a.		
C. senilis[a]	0.9	smooth			few, 12	40–55		
C. chrysacanthus	20	rough			many, 12	110–185		38
C. leucocephalus	4.2	smooth			many, 15	220–275		33
C. alensis	7.0	nearly smooth				90–125		29
C. royenii	8.5	nearly smooth			many, 15	90–140		44
C. nobilis	2.2	smooth			many, 6	75–90		24
Anisocereus lepidanthus	0.9	smooth			many, 6	<50		

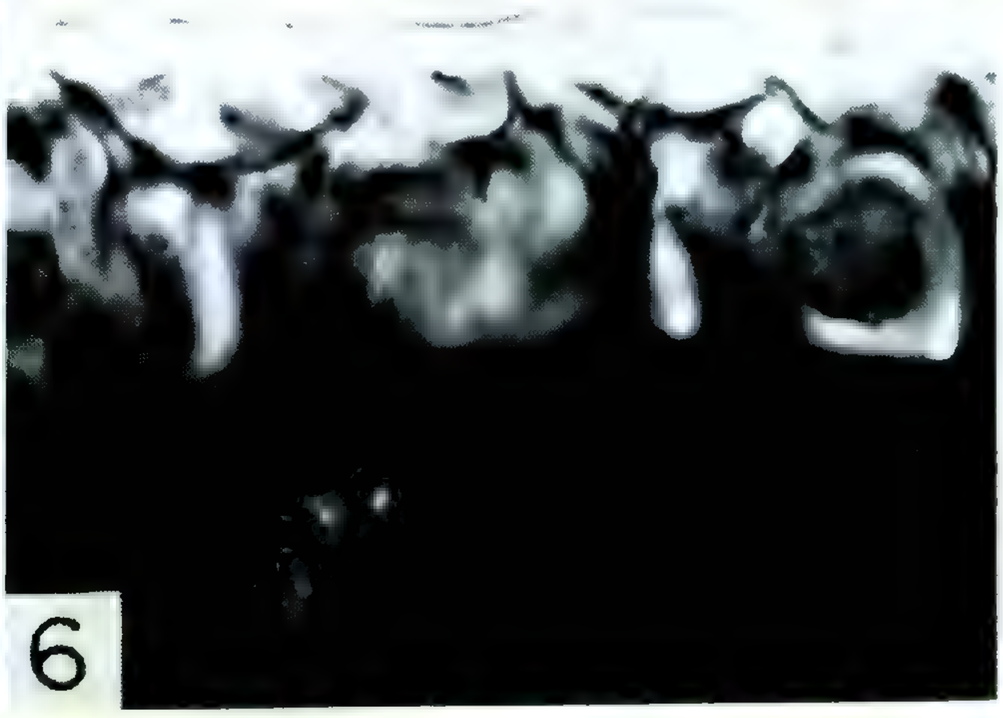
TABLE 2. Continued

Taxon	Maximum Cuticular Thickness (μm)	Cuticular Features (see text)	Type of Multiple Epidermis (see text)	Epidermal Silica Bodies, Range of Diameters (μm)	Epidermis Prismatics: No./Cell, Maximum Length (μm)	Hypodermal Thickness, Range of Diameters (μm)	Hypodermal Silica Bodies, Range of Diameters (μm)	Hypodermal Solitary Prismatics, Maximum Length (μm)
Columnar and other cacti assigned by Buxbaum to tribes other than Pachycereeae								
Acanthocereus horridus	2.9	smooth			one, 15	65–90		
A. pentagonus	3.5	smooth			one, 30	100–125		
A. subinermis	2.6	smooth			one, 18	130–155		
Armatocereus humilus	9.0	smooth	bullate clusters		one, 24	135–190		
A. laetus	12	rough; epicuticular wax				340–450		
Bergerocactus emoryi	3.9	slightly rough			many, small	65–80		
Cereus aethiops	3.9	rough				120–175		
C. dayamii	4.8	rough				250–340		
Ferocactus robustus	3.4	smooth				65–90		
Harrisia martinii	5.8	slightly rough				35–55		
H. pomanensis	3.5	nearly smooth				110–130		
Leptocereus quadricostatus	3.5	smooth			one, 24	130–155		
Monvillea cavendishii	1.1	smooth				55–70		
Nyctocereus chontalensis	2.9	smooth; epicuticular wax				35–55		
N. serpentinus	2.9	smooth				55–70		
Samaipaticereus corroanus	3.9	smooth	internal divisions			110–155		
Stetsonia coryne	6.3	slightly rough				110–135		
Trichocereus spachianus	5.6	smooth	internal divisions			100–125		
T. thelegonus	2.6	smooth	internal divisions			110–125		

[a] Quantitative measurements were taken from seedlings or very young plants, which do not have fully developed skin features.
[b] This species is represented only by a skin clearing from a dead specimen.







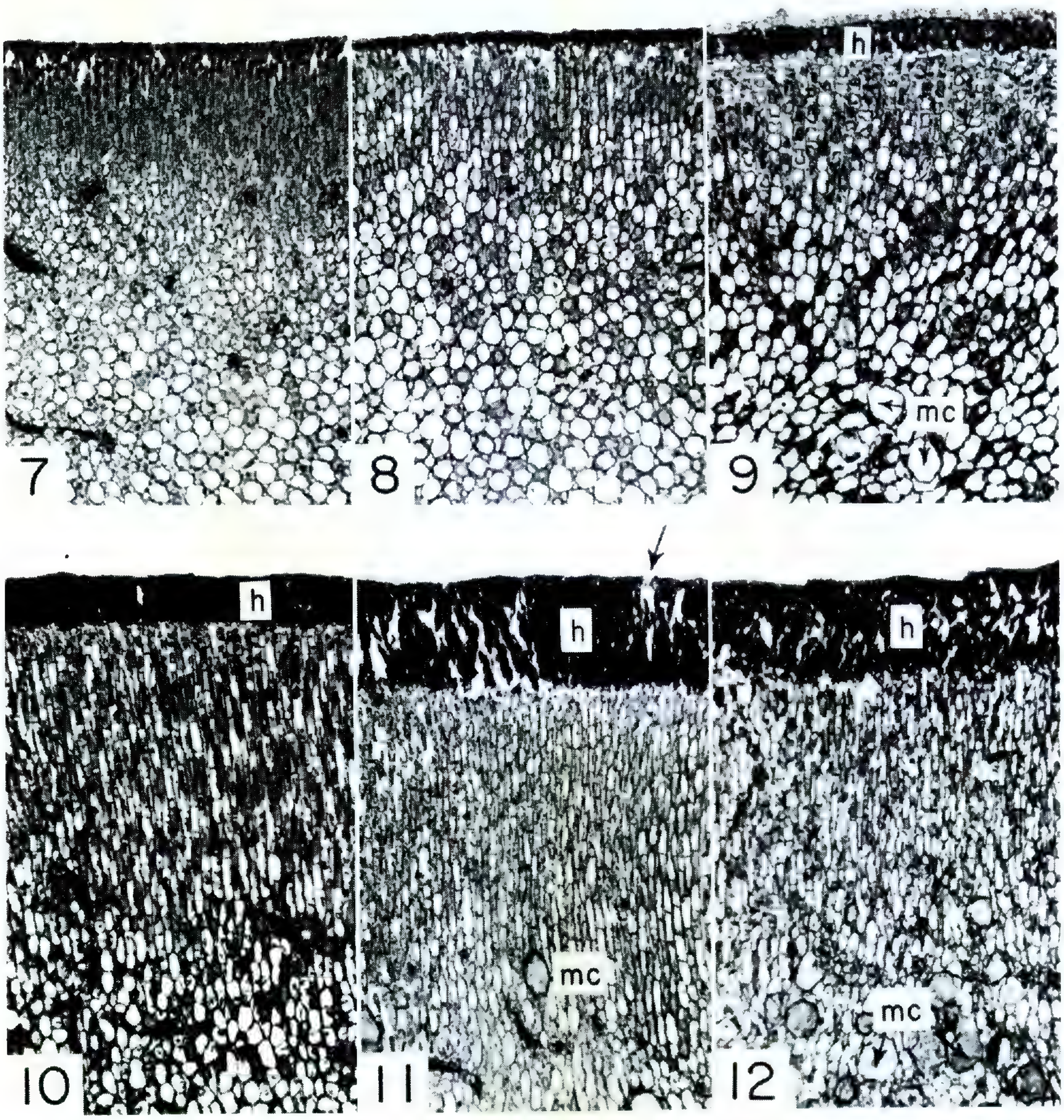
FIGURES 1–6. Skin features of Pachycereeae.—1–2. *Polaskia chende*.—1. Transection of stem surface, showing minutely bullate epidermal cells covered by thin cuticle and with very thin hypodermis (h). Note around substomatal chamber (sc) hypodermis is bilayered. ×560.—2. Surface view of cleared skin, showing groups of proliferated epidermal cells separated by thicker deposits of cuticle. ×170.—3. *Lophocereus schottii*; transection of skin, which has small bullate clusters, prominent cuticle, and occasional, strongly flattened calcium oxalate crystals that have hexagonal faces. ×560.—4. *Stenocereus hystrix*; transection of epidermis with internal periclinal divisions of the original single layer (arrow). Small silica bodies are barely visible in these cells. ×560.—5. *Carnegiea gigantea*; transection of epidermis showing multiple layers of cells covered by a very thick cuticle. ×560.—6. *Pachycereus marginatus*; transection of outer skin in which the outer epidermal walls are hornlike, extending into the thick cuticle. ×560.

Mature epidermal cells are commonly squarish to slightly tabular in transection, but in *Ferocactus robustus* cells are large and palisadelike. In surface view, the ground mass epidermal cells may have straight to wavy anticlinal walls, depending on the species, but cells are never markedly elongate.

Stomatal apparatuses superficially appear paracytic, similar to those of *Pereskia* (Bailey, 1964); however, meristemoid development needs to be described for columnar cacti. Guard cells are most commonly transverse to the long axis of the shoot (Metcalfe & Chalk, 1960). In columnar cacti, stomata are not deeply sunken except in *Escontria chiotilla*, *Pachycereus pecten-aboriginum*, and *P. pringlei*; in fact, guard cells often appear above the level of the ground mass cells in many species.

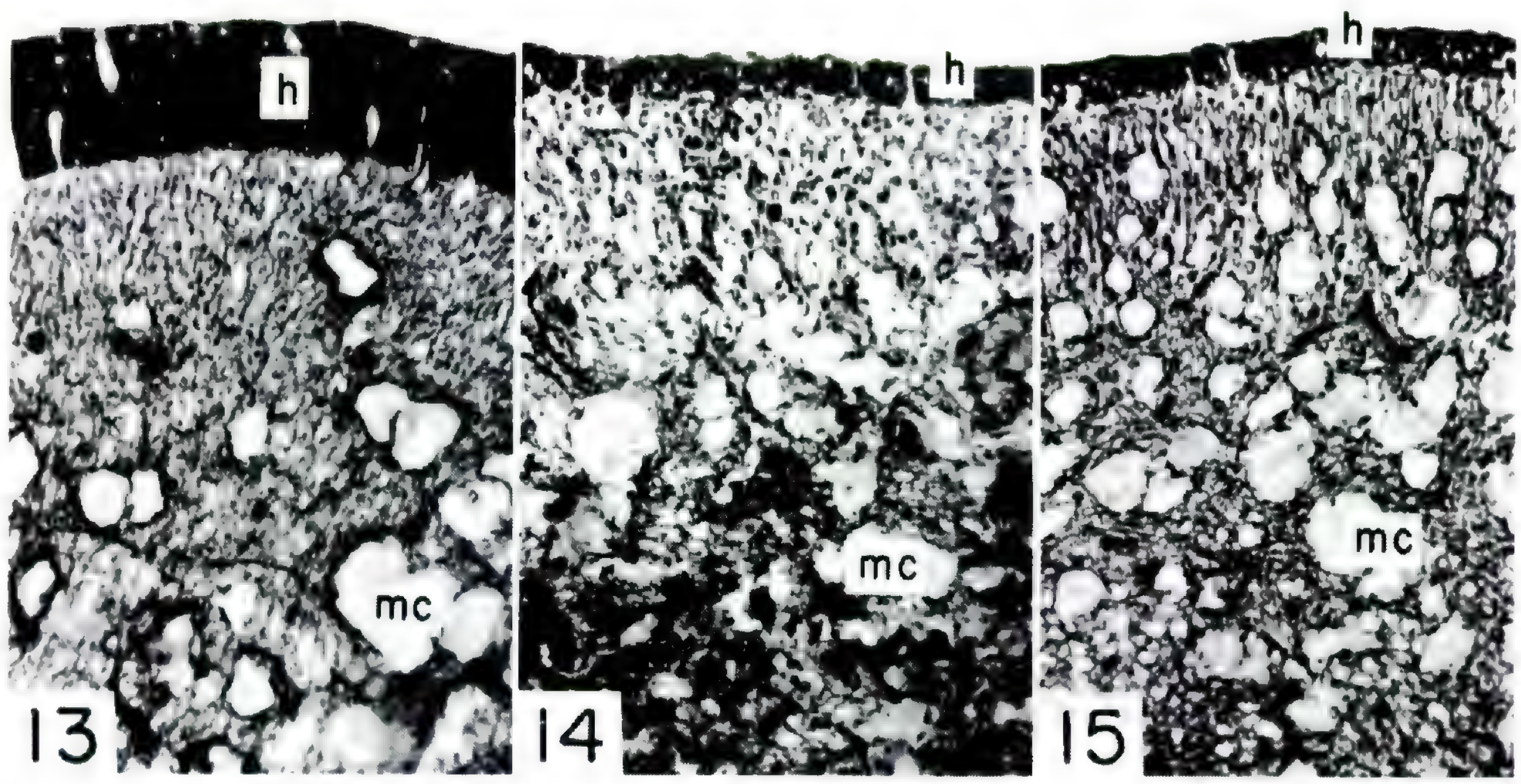
In transection, the cuticle proper (sensu Esau, 1965) in the majority of species is relatively thin and smooth and follows cell contours (Table 2); and within each genus closely related species have a cuticle of very similar thickness and characteristics. Species with hornlike projections from the outer periclinal walls have a thick, rough cuticle that completely covers the projections (Fig. 6), the taller the horns the thicker the cuticle. A thick to very thick, often rough cuticle is characteristic of numerous Pachycereeae that lack triterpenes. The most interesting cuticles are those with regular surface reliefs such in *Pachycereus weberi*, which has one central cuticular ridge above each cell; *P. pringlei* has a series of wavelike ridges opposite vertical anticlinal walls; *Carnegiea gigantea* has a series of parallel striations or ridges radiating from each stomatal apparatus, much as found in *Pereskia* (Bailey, 1964); and *Mitrocereus fulviceps* has a highly reticulate ridge system opposite anticlinal epidermal walls. Epicuticular wax is generally not observable with light microscopy in liquid-preserved materials of these species but is definitely present in *Armatocereus laetus*, *Cephalocereus chrysacanthus*, *Lophocereus schottii*, *Neobuxbaumia tetetzo*, *Nyctocereus chontalensis*, and *Stenocereus beneckei*. Preliminary observations indicate that these crystalline surface structures are relatively diverse in form and distribution and may be useful for systematic purposes when studied intensively with scanning electron microscopy.

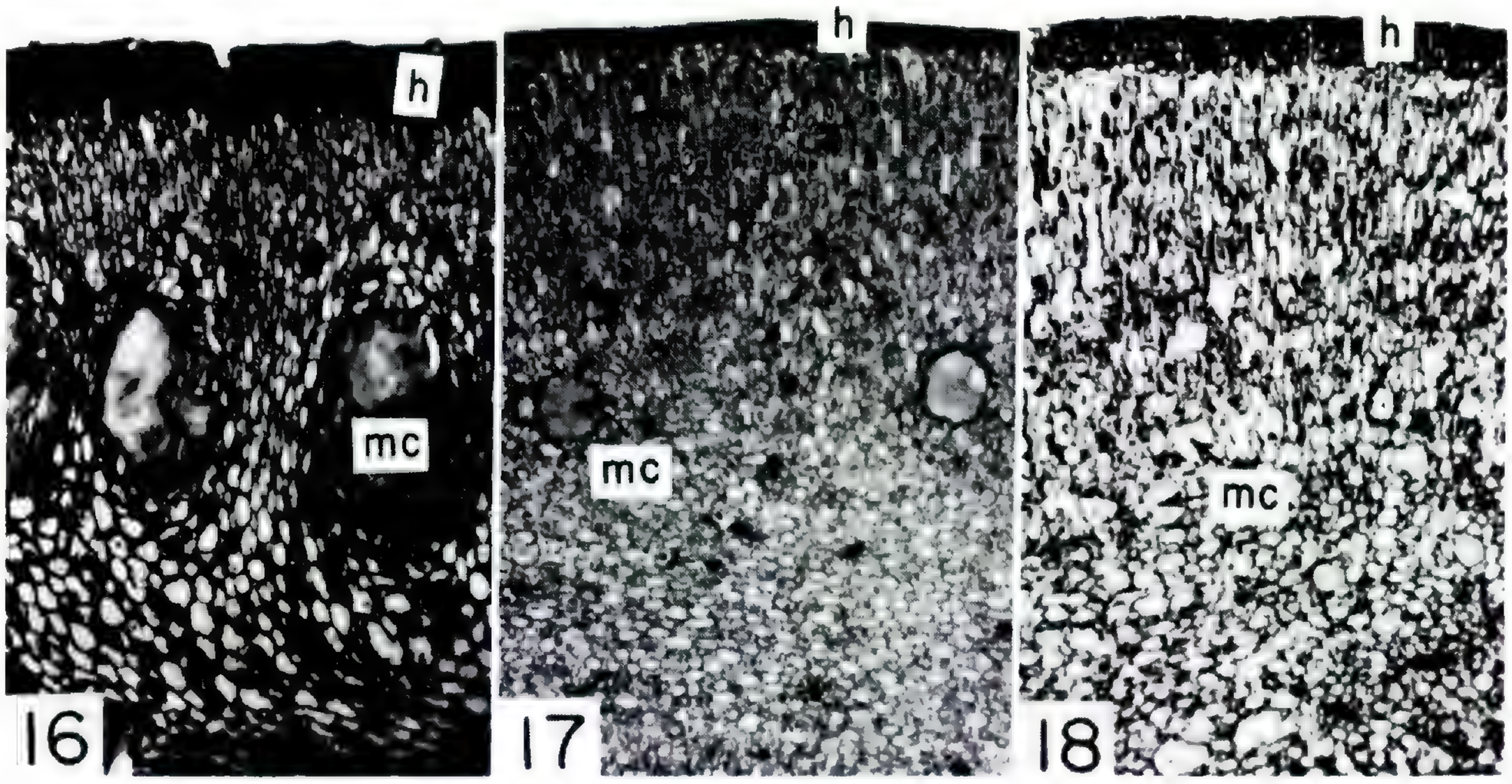
Beneath the epidermis lies a collenchymatous hypodermis (Figs. 1, 7–18), the so-called pseudohypodermis of Metcalfe & Chalk (1950), which ranges in thickness from one cell in *Anisocereus lepidanthus*, *Pachycereus hollianus*, young specimens of *Lophocereus gatesii* and *Pachycereus pecten-aboriginum*, *Polaskia chende* (Figs. 1, 8), and *P. chichipe* (Fig. 7) of Pachycereeae and *Harrisia martinii* of Hylocereeae to 12 or more cells in *Carnegiea gigantea* (Fig. 11), *Myrtillocactus cochal* (Fig. 13), *M. schenckii*, *Pachycereus pringlei*, and *P. weberi* (Fig. 12) of Pachycereeae and *Armatocereus laetus* of Leptocereeae. Hypodermal thickness in Table 2 is in micra, a rough indicator of the number of cell layers. Species with the thinnest hypodermises generally also have the thinnest hypodermal walls, e.g., in *Lophocereus gatesii* (Fig. 3) and *Polaskia* (Fig. 1); single-layered hypodermis is often composed of tangentially flattened cells with lamellar primary thickenings. In species with more than one collenchymatous layer, cells are mostly isodiametric and lack intercellular spaces. The hypodermis of *Pachycereus weberi* (Fig. 12) is unusual in that



FIGURES 7–12. Transections of stems of Pachycereeae, showing thickness of hypodermis (h) and distribution of mucilage cells (mc) in the outer rib. ×12.—7. *Polaskia chichipe* with thin hypodermis and no mucilage cells.—8. *Polaskia chende* with thin hypodermis and no mucilage cells.—9. *Lophocereus schottii* with relatively thin hypodermis and a few scattered mucilage cells.—10. *Pachycereus marginatus* with medium hypodermis and no mucilage cells. Note the elongate chlorenchymatous cells of the outer rib.—11. *Pachycereus pringlei* with very thick hypodermis, sunken stomates (arrow), and few, scattered mucilage cells far from the hypodermis. Note elongate chlorenchyma cells.—12. *Pachycereus weberi* with very thick hypodermis and scattered mucilage cells far from the hypodermis.

cells are markedly elongate in the radial plane and are retained in their original radial files. Hypodermal cells have prominent primary pit-fields, the so-called conspicuous intercellular pitting of Conde (1975). In species with very thick skins, hypodermis may be twice as thick in the valleys as on the flat surfaces of the ribs and thinnest in the vicinity of each areole. Collenchyma in columnar cacti is capable of undergoing decrease in wall thickness and dedifferentiation





FIGURES 13–18. Transections of stems of columnar cacti, showing relative thickness of hypodermis (h) and distribution of mucilage cells (mc) in the outer rib. ×12.—13. *Myrtillocactus cochal* with thick hypodermis and scattered large mucilage cells throughout the rib.—14. *Stenocereus standleyi* with relatively thin hypodermis and abundant, closely packed mucilage cells throughout the rib.—15. *Stenocereus beneckei* with relatively thin hypodermis and numerous, closely spaced mucilage cells.—16. *Stenocereus thurberi* with medium hypodermis and very large mucilage cavities located around the outer rib cortex.—17. *Acanthocereus horridus* with relatively thin hypodermis and a few, widely spaced mucilage cells far from the hypodermis.—18. *Cereus dayamii* with a relatively thin hypodermis and relatively small, well-spaced mucilage cells throughout the rib.

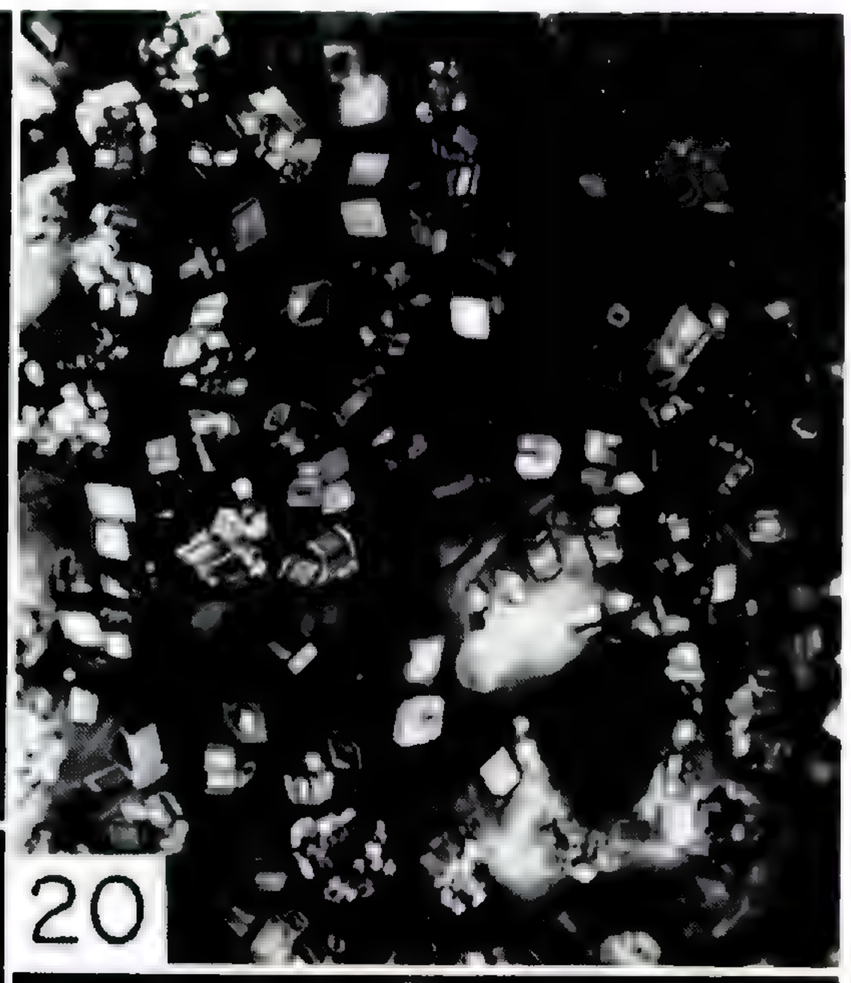
into parenchyma for initiation of phellogen. No cactus hypodermis has ever been found with lignified walls at maturity (Conde, 1975; Gibson, unpubl. data).

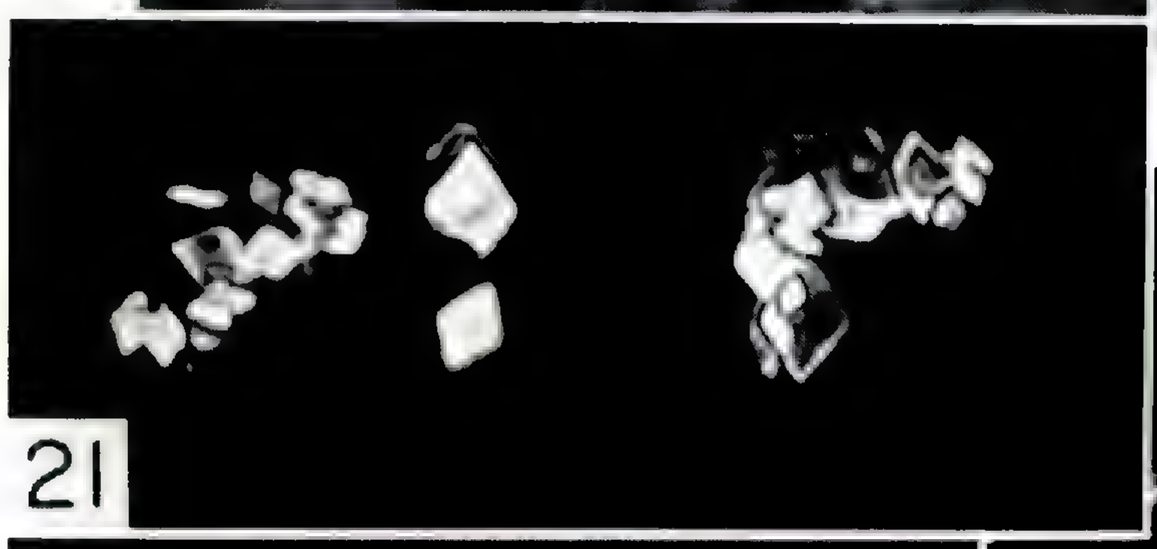
Collenchyma is interrupted at regular intervals by substomatal canals that

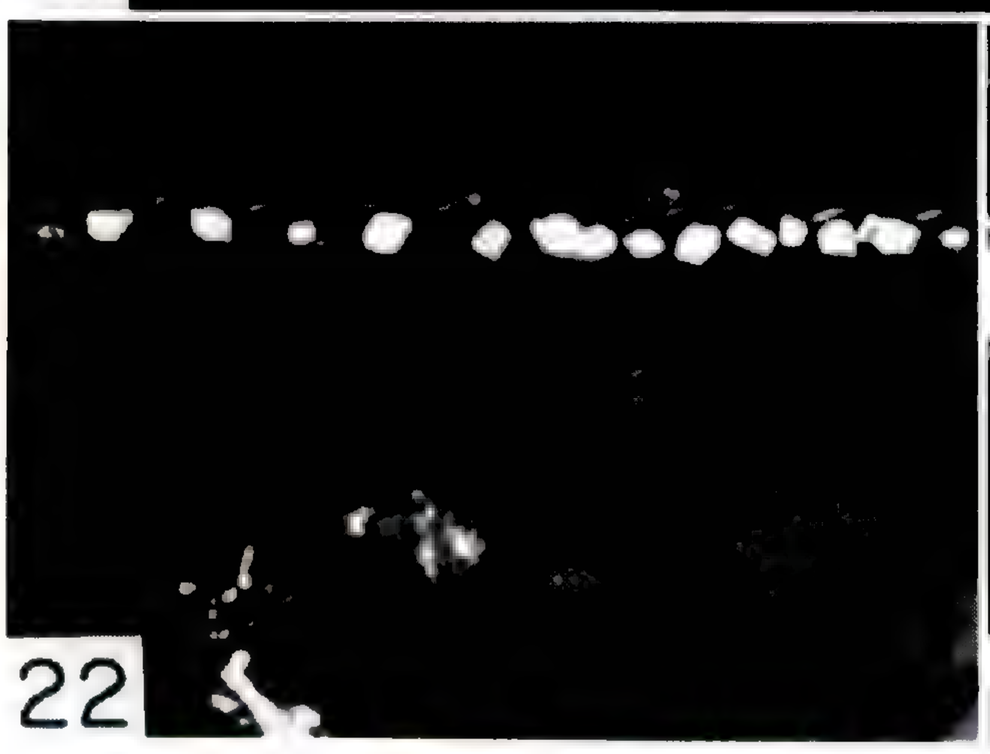
extend from the guard cells to the chlorenchyma. In species with a single-layered hypodermis, two collenchymatous cells are generally found beneath the guard cells (Fig. 1).

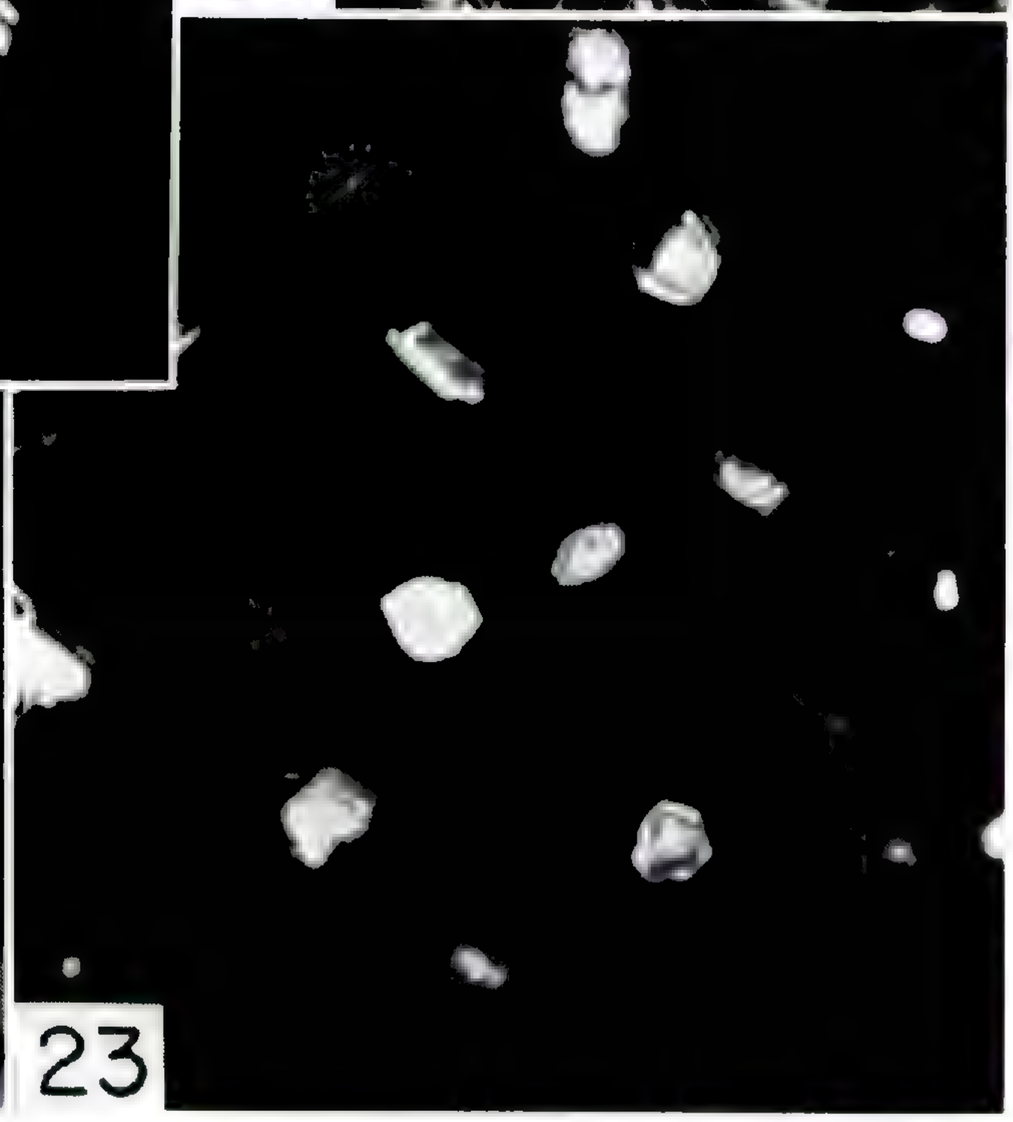
Among the species examined from North and South America, 17 species (Table 2), namely, all species of *Stenocereus* included in this study and "*Lemaireocereus thurberi* var. *littoralis*," have silica bodies in the skin (Fig. 19). They are found in both the epidermis and hypodermis of 13 species, only in the hypodermis of two species, and only in the epidermis of three species. In stained microslides of *Stenocereus alamosensis*, S. *beneckei*, and S. *kerberi*, hypodermal silica bodies are small and infrequent and can easily be overlooked; therefore, absence of these structures in hypodermis of several other species of *Sternocereus* is not certain. Only one silica body is present per cell, and they are absent in the stomatal guard cells. In species of *Stenocereus* with more than one epidermal layer, every epidermal cell contains a silica body. Size and morphology of silica bodies vary between species (Table 2), between specimens, and even from outer to inner portions of the skin of the same rib. In our materials, S. *gummosus* has the largest silica bodies, which have very prominent branched projections (Fig. 19). Large spheroidal hypodermal silica bodies with short but prominent arms are found in S. *stellatus*, S. *thurberi*, and S. *treleasei*, but of these species only S. *thurberi* has epidermal silica bodies. These inclusions in other species of *Stenocereus* are often irregular in shape and have shorter, narrower, and more numerous projections. Size of hypodermal silica bodies generally decreases from the outside to the inside of the skin, and in some species the innermost hypodermis possesses few, if any, silica bodies.

One-third of the species investigated have prismatic calcium oxalate crystals in the skin (Table 2), and the occurrence of silica bodies and calcium oxalate crystals in the skin is mutually exclusive. Half the species of Mexican Pachycereeae that lack triterpenes have many small rhomboidal crystals in each ground-mass epidermal cell (Figs. 20–21). These crystals are extremely similar in size and shape in seven species of *Cephalocereus* (including the type, *C. senilis*), in *Mitrocereus*, and in *Neobuxbaumia*. *Mitrocereus fulviceps* is unusual in that these crystals are found in many, but not all, epidermal cells. *Carnegiea* has numerous small birefringent bodies in each epidermal cell that are probably prismatic crystals. *Anisocereus lepidanthus* has crystals that tend to be squarish or rectangular in outline and are smaller than those in *Cephalocereus*; and *Lophocereus gatesii* has few, extremely flat crystals that are hexagonal on the largest facets (Fig. 3). In contrast, crystals in the epidermis of *Acanthocereus* (Fig. 22), *Armatocereus*, and *Leptocereus* are generally large, rhomboidal, and solitary. Large prismatic calcium oxalate crystals, usually one per cell, are found in the hypodermis of four species of *Cephalocereus* (Fig. 23), including one of the two species that lacks epidermal crystals, and *Mitrocereus fulviceps*. Stellate druses occur in every cell of the outermost hypodermal layer in *Monvillea cavendishii* of Cereeae. *Stetsonia coryne* is the only species other than Pachycereeae that has hypodermal crystals, and these are extremely large and do not closely resemble those of Pachycereeae in shape.









FIGURES 19–23. Ergastic inclusions in skin of columnar cacti.—19. *Stenocereus gummosus*; transection of hypodermis in which large silica bodies (sb) with prominent arms are found, 1 per cell. ×450.—20. *Cephalocereus hoppenstedtii*; surface view of cleared skin of a dead specimen in polarized light, showing few to many prismatic calcium oxalate crystals in each ground-mass epidermal cell. ×140.—21. *Cephalocereus totolapensis*; transections of epidermis in polarized light, showing numerous prismatic, calcium oxalate crystals in each ground-mass epidermal cell. ×500.—22. *Acanthocereus pentagonus*; transection in which a large prismatic, calcium oxalate crystal occurs in each ground-mass epidermal cell. ×140.—23. *Mitrocereus fulviceps*; transection of valley of stem in which one calcium oxalate crystal occurs in each hypodermal cell. Numerous prismatic crystals are found occasionally in epidermal cells of this species on the ribs. ×350.

Wild-collected plants differ from cultivated plants of the same species in having thicker cuticle, hypodermis, and hypodermal walls; more numerous epidermal proliferations; and slightly larger or more numerous ergastic inclusions. Therefore, anatomical differences between species of the same genus may not be as clear as indicated in Table 2; nevertheless, data in the table can be used to identify sterile materials correctly to genus and often to species. Broad sampling

of natural populations will be needed to obtain maximum and minimum values for skin features.

CORTICAL GROUND TISSUE

A variety of textures of cortical (including rib) ground tissue may be observed when fresh stems of cacti are cut. In columnar cacti cortical textures range from firm or even hard and nonmucilaginous to firm, very spongy, or soft but highly mucilaginous. Some species are so mucilaginous that specimens with the skin removed slip easily from the hands. This range of textures, which includes all degrees of mucilage accumulation, corresponds at the anatomical level to differences between species in number, size, and distribution of idioblastic mucilage cells and crystal-bearing cells. In Pachycereeae the simplest condition, where neither mucilage nor crystalliferous cells are present in the cortex, is found in *Pachycereus hollianus*, *P. marginatus* (Fig. 10), *Polaskia chende* (Fig. 8), *P. chichipe* (Fig. 7), and *Pterocereus gaumeri*; *Anisocereus lepidanthus* is nonmucilaginous but has large solitary prismatics scattered throughout the cortex. As discussed in the previous section, all of these species except *P. marginatus* have a one-layered or thin hypodermis, and all but *A. lepidanthus* lack crystals in the skin. Other species of *Pachycereus* and *Mitrocereus fulviceps* have moderately sized and widely spaced mucilage cells in the ribs, generally 1 mm or more from the hypodermis (Figs. 11–12), and of these species only *P. weberi* has a significant number of scattered mucilage cells in the cortex. Cells bearing large to very large aggregates of cuboidal or rhomboidal crystals occur in the cortex of these arborescent Pachycereeae but are unusually abundant in the cortex of *M. fulviceps*, giving this ground tissue a granular texture. Large nests of crystal aggregates are also present in *Neobuxbaumia* and *Cephalocereus totolapensis*, which have moderately sized mucilage cells widely spaced throughout the cortex. Both species of *Lophocereus* have nearly nonmucilaginous cortical ground tissue, the few scattered mucilage cells occurring at the base of the ribs (Fig. 9). All other Pachycereeae examined have abundant mucilage structures. For the species listed in Table 1, which also includes all species with silica bodies in the skin, three designs of mucilage-cell distribution are observed: (1) medium to relatively large mucilage cells that are generally evenly spaced in the main stem and the ribs but are not abundant near the hypodermis, as in *Escontria* and *Myrtillocactus* (Fig. 13); (2) medium to large mucilage cells that are abundant and often closely packed throughout the main stem and rib cortex and are generally found near the hypodermis, as in most species of *Stenocereus* (Figs. 14–15); and (3) extremely large mucilaginous sacs located beneath the hypodermis, only in *S. thurberi* (Fig. 16). The remaining species, belonging to *Cephalocereus* and *Carnegiea gigantea*, have abundant moderately sized mucilage cells distributed throughout the cortex, much as in *Stenocereus*. Many species of *Stenocereus* have large aggregates of cuboidal crystals near the stele and scattered crystal aggregates in the center of the rib.

Of the other 20 species examined, *Ferocactus robustus* of Cacteae, *Monvillea cavendishii* and *Stetsonia coryne* of Cereeae, and *Harrisia pomanensis* and species of *Nyctocereus* of Hylocereeae are nonmucilaginous. In *S. coryne* small to mod-

erately sized crystal aggregates are present throughout the cortex, and within the ribs individual cells or groups of cells form lignified secondary walls in old stems. *Harrisia pomanensis* has large crystal aggregates, mostly in the ribs, whereas *Nyctocereus serpentinus* has them restricted to regions near the stele. In contrast, *N. chontalensis* has abundant delicate stellate druses of acicular crystals, primarily in the ribs; similar acicular crystals are also observed in *Eccremocactus* and *Hylocereus*, epiphytes of the same tribe (unpubl. data). In species of *Acanthocereus* of Hylocereeae, widely spaced cortical mucilage cells are observed near the stele and in two species occasionally in the ribs (Fig. 17). *Acanthocereus pentagonus* and *A. subinermis* have some stellate druses scattered throughout cortical ground tissue. *Leptocereus quadricostatus* of Leptocereeae has relatively few scattered mucilage cells in the cortex, but nearly every parenchyma cell contains either a large solitary crystal or a crystal aggregate, giving this tissue a hard, granular texture similar to that of *Mitrocereus fulviceps*. The mucilage cells of *Samaipaticereus corroanus* are restricted to the ribs, and crystals are generally absent. In species of *Armatocereus*, which undoubtedly are related to Pachyceereae, cortical mucilage of *A. humilis* is similar to that of *Myrtillocactus* and cortical mucilage of *A. laetus* to that of the large arborescent species of *Pachycereus*. Other columnar cacti have highly mucilaginous stems with numerous mucilage cells, evenly distributed throughout the cortex (Fig. 18), much as in *Cephalocereus* and most species of *Stenocereus*. The most mucilaginous are *Bergerocactus emoryi* and *Trichocereus thelegonus*, which have large mucilage cells near the hypodermis. Even though the patterns of mucilage cells of *Cereus* are superficially similar to those of Pachycereeae, the ground tissues of these taxa are dissimilar in texture and anatomical appearance. In-depth comparisons between unrelated species with similar mucilage cell and crystal patterns are premature because tissue morphology is undoubtedly affected by differences in age and chemical composition.

In cactus stems, cortical ground tissue is bright green directly beneath the translucent skin and paler toward the inside. Chlorenchyma is densest and chloroplasts are largest in the first subskin layers. Particularly in stems where mucilage cells are not found close to the skin or are completely absent from the ribs, the files of chlorenchymatous cells are well developed (Figs. 7–8, 10–12) and remain intact even after bark forms on the green stems. In the arborescent species of *Pachycereus* (Figs. 10–12) and in *Stetsonia coryne*, chlorenchymatous cells are markedly elongate in the radial direction.

In Cactoideae, cortical ground tissue is vascularized by an elaborate system of bundles, which are more or less independent in development from the principal primary vascular system of the shoot. To date, the three-dimensional nature of this system in columnar cacti has not been studied. In Pachycereeae, the most extensive systems occur in the most succulent plants. Mucilage cells generally are not found any closer to the hypodermis than are the cortical bundles, and throughout the cortex mucilage cells are nearly always next to the phloem of these bundles. The close proximity of mucilage structures to phloem suggests that in these species sugars for mucilage production are directly supplied from the phloem. Cortical vascular bundles generally lack primary pholem fibers,

even in old stems, but such fibers are conspicuous and precocious in *Acanthocereus horridus*, *Bergerocactus emoryi*, and *Stenocereus stellatus*.

STELE

In transection the stele of most columnar cacti consists of a ring of several dozen to over 200 collateral bundles surrounding a pith. Within a tribe, the number of bundles present is a function of stem diameter, number of ribs, and diameter of the pith; those species with the widest pith and most ribs have the most stelar bundles. Bundles of the vascular cylinder occur in sets, being concentrated opposite the stem valleys and not the ribs; therefore, the number of sets of bundles is equal to the number of stem valleys (or ribs), and the sets are separated by parenchyma. Largest bundles of each set occur in the center, and bundle size decreases gradually away from this point. In Pachycereeae, each set is solidly joined by secondary growth so that the first-formed system is a ring of parallel rods, one per valley (Gibson, 1978). This design accommodates late expansion of the pith. These rods may fuse into a solid cylinder of wood when pith enlargement stops, giving the vascular cambium time to become completed across the parenchymatous regions. However, in arborescent species with extremely wide pith, e.g., in *Carnegiea gigantea* and *Pachycereus pringlei* (categories IA–IC and IE of the earlier section), rods of wood are discrete for many years, generally being separate to near the trunk or base (solitary columnar forms) of mature trees. This pattern of wood formation as rods is characteristic of only Pachycereeae (Gibson, 1978); in fact, each tribe of Cactoideae appears to have its own basic architectural design of primary vasculature and wood skeletons even though external features are convergent.

Primary phloem fibers are found in all columnar cacti in this study; however, comparisons between specimens with similar amounts of secondary growth show that phloem-fiber formation is precocious in some species. Species in the following genera show relatively late differentiation of phloem fibers: *Anisocereus*, *Armatocereus*, *Carnegiea*, *Cephalocereus*, *Escontria*, *Lophocereus*, *Mitrocereus*, *Myrtillocactus*, nonmucilaginous species of *Pachycereus*, *Polaskia*, *Pterocereus*, and *Stenocereus dumortieri*, *S. thurberi*, and *S. treleasei*. This list includes all of the species of Pachycereeae with nonmucilaginous or slightly mucilaginous stems. Precocious development of primary phloem fibers, well in advance of secondary growth, is found in species with many different growth habits, e.g., *Acanthocereus*, *Bergerocactus*, *Stenocereus stellatus*, and *Pachycereus weberi*; so there appear to be no strong correlations between plant size and degree of development of phloem fibers. Nevertheless, fibers differ in length, width, and wall thickness between species, and some correlations may exist between design of the plant and tissues and the nature of phloem fibers. No sclerenchyma occurs in secondary phloem of columnar cacti.

One avenue of evolution for succulence in columnar cacti has been the enlargement of pith. As indicated in a previous section, size of the pith is generally correlated with type of growth form and habit; and, in general, species with the most extreme growth habits in a genus, e.g., very large arborescent species, have the widest pith of the phylad. Pith typically has a vascular system; but this

system is poorly developed in *Leptocereus quadricostatus* (Leptocereeae) and completely lacking in *Ferocactus robustus* (Cacteae) and in *Acanthocereus*, *Nyctocereus chontalensis*, and *Peniocereus* (Hylocereeae). Of the Pachycereeae with medullary systems, pith mucilage cells are absent in all species of *Anisocereus*, *Lophocereus*, *Mitrocereus*, *Neobuxbaumia*, *Pachycereus*, *Polaskia*, and *Pterocereus*, and also in *Cephalocereus russelianus* and *C. totolapensis*. As noted before, these species have little or no mucilage in the cortex. Mucilage cells are relatively few, small, and scattered in the pith of other species of *Cephalocereus* as well as in *Escontria* and *Myrtillocactus*. Walls of pith cells in *Pachycereus weberi* are surprisingly thick but still unlignified. Other Pachycereeae have mucilaginous pith, especially in *Stenocereus*. In *Stenocereus*, *S. deficiens*, *S. dumortieri*, and *S. pruinosus* have the fewest and smallest mucilage cells. In tribes other than Pachycereeae, pith mucilage cells are generally abundant and well spaced except in species that lack mucilage in the cortex. Species of *Acanthocereus* have numerous, widely spaced mucilage cells in the pith but lack medullary vasculature, showing that mucilage cells can differentiate apart from vascular bundles. In general, however, medullary bundles are present where pith mucilage occurs.

STORAGE OF STARCH IN THE STEM

Some estimates of the general distribution of starch in a stem can be made by staining transections of entire cactus stems with IKI. Although amount of starch probably varies in different parts of the plant and in different seasons, some definite distributional trends were observed in the specimens examined. In stems without mucilage cells in the cortex and pith and with relatively narrow pith, starch grains accumulate most often in the inner cortex, primary phloem, medullary rays, and outermost cell layers of the pith; whereas in species with large pith containing numerous mucilage cells, starch grains in the pith are not only very abundant but also very large. Exceptions are *Pterocereus* and *Anisocereus*, which have extremely large compound starch grains concentrated in the narrow pith; *Stenocereus thurberi*, which has numerous large starch grains in the ribs as well as in the pith; and species of *Armatocereus*, and certain species of *Cephalocereus*, *Myrtillocactus schenckii*, and *Pachycereus marginatus*, which show no concentration of starch in any specific tissue. Thus, enlargement of the pith seems paralleled by increased utilization of pith for starch storage. However, some species with narrow pith apparently have arisen from species with larger pith yet still store starch in the pith, e.g., in certain narrow-stemmed taxa of Hylocereeae. An intensive study of these ergastic substances may provide important systematic information.

Morphology of Reproductive Structures

GENERAL FEATURES

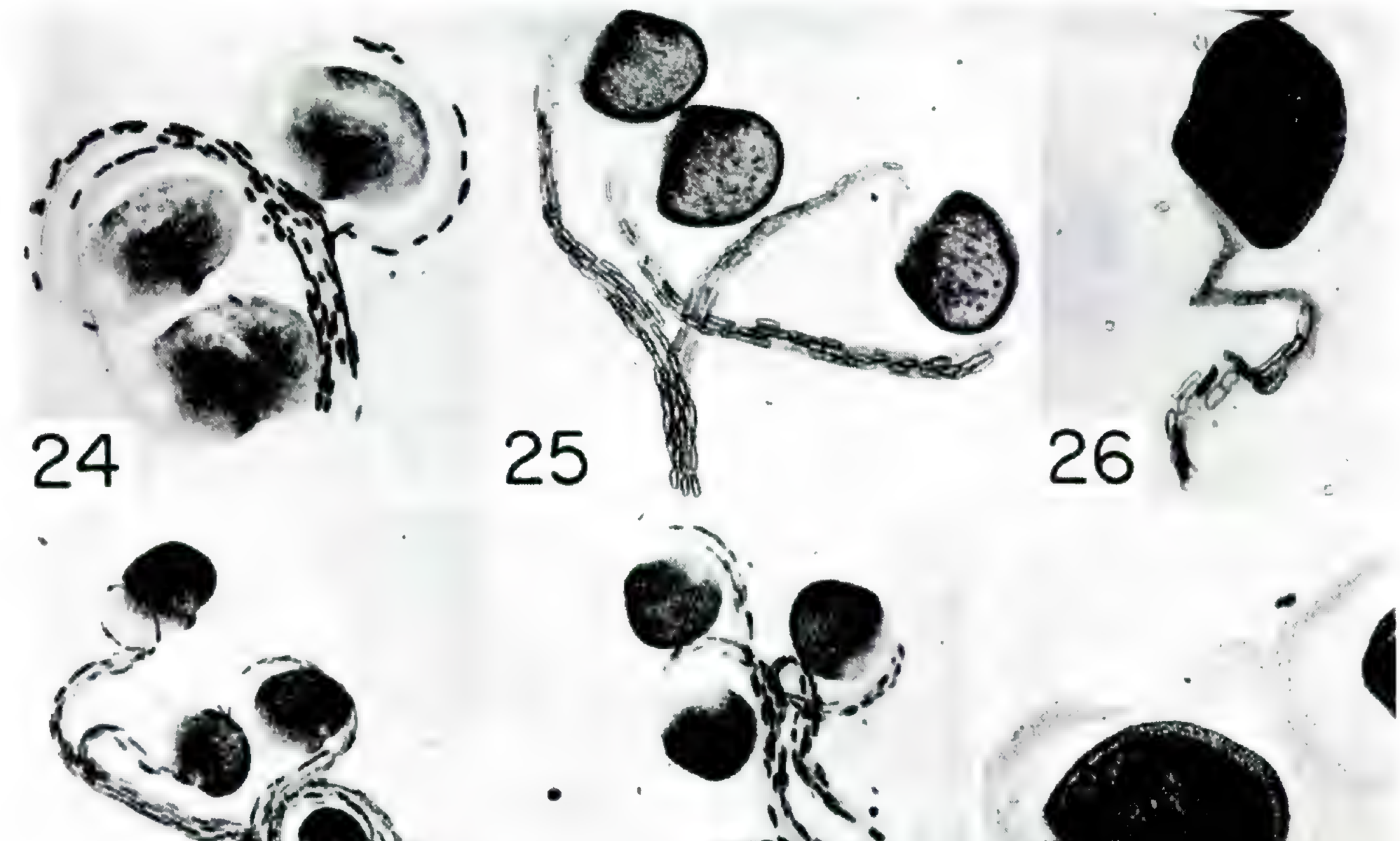
Boke (1964) has conclusively shown that epigyny in cacti has resulted from the pulling downward of the ventral sutures of numerous carpels with axile placentation so that the bases of the carpels are not at the bottom of the locule

and placentation appears parietal. Therefore, in the typical epigynous cactus flower the ovary is covered by stem tissue and the floral tube actually begins above the level of the multicarpellate locule. Buxbaum (1953) has coined the term "pericarpel" for the stem tissue covering the ovary that later becomes the outer pericarp. Cactus flowers are always solitary, borne on axillary buds (areoles), but a few species have long-lived condensed spur shoots on which several flowers may arise from several axillary buds of areolar spines.

In columnar cacti no external distinction can be seen between the pericarpel and floral tube because nodes on both are produced in the same helical phyllotactic sequence. The leaf bases (podaria) are most commonly enlarged and often decurrent, especially on the floral tube, and their laminae are often very reduced. Axillary buds of these primordia most commonly have tufts of soft trichomes and may have either rigid spines or more flexible bristles. The size and morphology of podaria, laminae, and areolar features change in a graded series from older to younger nodes, the younger primordia becoming weakly differentiated sepaloid and petaloid perianth parts. Color of the flower also grades from the darkest, generally greenest, shades on the podaria of the floral tube toward the inner perianth parts. Adnate to the floral tube are 100 to several thousand helically arranged stamens, which have long filaments and basifixed anthers that dehisce tricolpate pollen grains through longitudinal slits. A nectary chamber forms below the stamens around the lower part of the style. The unilocular multicarpellate pistil generally has numerous branched funiculi, each bearing four or more anatropous ovules, and a long, thick style with a multipartite papillate stigma. After pollination, the floral tube and style shrivel but often are long persistent on the developing fruit, and the ovary with attached pericarpel matures into a large berry, often with red-colored pulp containing hundreds of dark brown or black seeds. During maturation of the fruit the diameter of the ovary increases several fold, and the external pericarpel features often change markedly, providing an interesting array of characteristics for classification.

TRITERPENE-BEARING PACHYCEREEAE

As noted in the introduction, Buxbaum (1962c) first observed in *Myrtillocactus* special pigment cells in the edipermis of funiculi which he termed pearl cells ("Perlzellen") because at maturity these cells are enlarged, looking like a string of colored pearls. In species that have these intensely colored cells, the pigment first appears before anthesis (Figs. 24–28). Only some of the cells of the epidermis contain the pigment, the rest remain colorless. This is in sharp contrast to pigmentation of the pulp in other species (Figs. 29–32), e.g., *Carnegiea gigantea* and *Lophocereus schottii*, in which the pigment is manufactured late in the ontogeny of the fruit and diffuses from the ovary wall via vascular strands into the cells of the pulp. Even though the chemistry of Buxbaum's pearl cells has not been studied, there are reasons to suspect that the pigment present at anthesis is not water soluble because it does not diffuse out of the cells when mounted in Hoyer's medium, fresh in water, or preserved in FAA, a fixative that includes water and ethanol. Similar pigment cells are found in the epidermis



FIGURES 24–32. Funiculi with anatropous ovules at or slightly after anthesis, mounted in Hoyer's medium. Differences in ovule size are not proportional to the final differences in seed size because ovules are not at the same stage of development. ×25.—24–28. Branches of funiculi with epidermal pigment cells.—24. *Stenocereus alamosensis*.—25. *Polaskia chende*.—26. *Escontria chiotilla*.—27. *Stenocereus thuberi*.—28. *Myrtillocactus cochal*.—29–32. Branches of funiculi with no pigment cells at anthesis.—29. *Stenocereus beneckei*.—30. *Cephalocereus hoppenstedtii*.—31. *Lophocereus schottii*.—32. *Pachycereus hollianus*.

of the perianth parts, inner floral tube, filaments, style, stigma, and, sometimes, the anthers of the same species that have the funicular pigment at anthesis, but this same pigment also colors floral parts of other Pachycereeae that lack the funicular pigments, e.g., *Lophocereus*.

To date, Buxbaum has reported special funicular pigment cells in *Heliabravoa* (1967, here as *Polaskia chende*), *Machaerocereus* (1968b, 1969), *Myrtillocactus* (1962c, 1972), *Polaskia* s.s. (1963d), *Rathbunia* (1975c, here as *Stenocereus*), and most species of *Stenocereus* (1963b, 1969). Buxbaum (1963b) observed that these pigment cells are absent in S. *beneckei*, S. *laevigatus*, and S. *weberi*, which he considers primitive species of the genus. Our observations confirm Buxbaum's list but also add *Escontria* and *Lemaireocereus thurberi* var. *littoralis*.

Both *Stenocereus marginatus* and *S. weberi*, here assigned to *Pachycereus*, lack these cells in our material, and *S. beneckei* lacks them in the immature flowers we have seen. No material of *S. laevigatus* was available for study; nevertheless, it is clear that only species with abundant stem triterpenes have these unusual funicular pigment cells in Pachycereeae and in Cactaceae as a whole. These are also the only reported cases of silica bodies in the stem.

Polaskia.—2 spp. (Backeberg, 1960; Bravo & Cox, 1958; Buxbaum, 1963d, 1967). Flowers borne at shoot tips, 1 per areole, diurnal, to 5 cm long, slightly wider than long when fully open; ovary and floral tube covered by numerous small but discrete podaria, each bearing a small but evident lamina, the areoles with conspicuous tan trichomes and light-colored bristles in *P. chende* but essentially naked in *P. chichipe*; floral tube short and narrow, to 1 cm long above the ovary; perianth spreading and inner parts pale pink (*P. chende*) or rotate to reflexed and yellowish green (*P. chichipe*), minutely serrulate along the upper margins; stamens numerous; style with 12 strongly papillate stigma lobes, exserted beyond the stamens; nectary chamber open; at anthesis, immature fruit 1.0–1.5 cm thick, the wall nonmucilaginous; red pigmentation present in the pericarpel and absent from the ovary wall and beneath the locule; locule spherical, about 4 mm thick. Fruit globular, 4 cm (*P. chende*) or 2.5 cm (*P. chichipe*) thick, generally lacking laminae but having clusters of short spines rather than bristles, some long trichomes persistent in *P. chende*; pericarp with few mucilage cells; pulp of mature fruit somewhat mucilaginous, sweet and red. Seeds very small, well spaced, pyriform-ovoid and subtruncate, with tan sublateral hilum; testa dull black and reticulate punctate.

Escontria.—1 sp. (Bravo, 1937; Buxbaum, 1970a; Marshall & Bock, 1941). Flowers borne at shoot tips, 1 per areole, diurnal, 3.5–4.0 cm long, narrowly cylindric-funnelform; ovary and floral tube covered by wide imbricated, chartaceous, yellowish but translucent scales (laminae) with minutely serrulate upper margins; floral tube about 1 cm long above the ovary; perianth erect, the parts narrow, yellow, minutely serrulate; stamens numerous; style with about 8 stigma lobes, included; nectary chamber somewhat closed; at anthesis, immature fruit about 1.5 cm thick, the wall usually nonmucilaginous; red pigmentation present in the thick pericarpel and absent from the ovary wall and beneath the locule; locule shieldlike in longisection, 6 mm or more wide. Fruit globular, 5 cm thick, covered by chartaceous scales of the original pericarpel and lacking trichomes or spines; pericarp with abundant mucilage cells; pulp of mature fruit deep purple red, sweet. Seeds very small (smallest of any Pachycereeae), similar to those of *Polaskia* but with more rugose testa.

Myrtillocactus.—4 spp. (Buxbaum, 1962c, 1972). Flowers several per areole, produced on old spur shoots on all green stems, diurnal, no more than 3 cm long, slightly wider than long when fully open; ovary and floral tube with few, low podaria, each with a small lamina, the spines and trichomes hidden or absent; floral tube extremely short and slightly flaring; perianth spreading to rotate, the parts grading from pale pinkish white in the center to purplish green on the outside; stamens relatively few; style with up to 6 stigma lobes, exserted when perianth rotate; nectary chamber very small, narrow, completely open;

at anthesis, immature fruit oblong, not more than 5 mm thick, the wall of the ovary and pericarpel relatively mucilaginous; red pigmentation present in the pericarpel and absent in the ovary wall and beneath the locule; locule oblong, 1–2 mm thick. Fruit oblong, to 2.5 mm long, mostly smooth with small laminae, each subtending a small tuft of light-colored trichomes and, sometimes, a very short, often inconspicuous spine; pericarp with abundant mucilage cells; pulp deep purple red and sweet. Seeds very small, widely spaced, similar in structure to those of *Escontria*.

Stenocereus.—ca. 22 spp. (Backeberg, 1960; Benson, 1969a; Bravo, 1937, 1956c; Britton & Rose, 1920; Buxbaum, 1955, 1963b, 1963d, 1968b, 1969; Gates, 1957; Martin, 1973; Sánchez Mejorada, 1972, 1973a; Shreve & Wiggins, 1964). Flowers borne mostly at shoot tips, except in *S. dumortieri* where borne far down the ribs, and in machaerocerei and rathbunias, where borne mostly on old areoles, 1 per areole, diurnal or nocturnal, 5–22 cm long, tubular-campanulate, funnelform, funnelform-campanulate, and narrowly salverform; ovary and floral tube with numerous podaria, often with long-decurrent bases on the floral tube, each usually bearing small laminae; podaria of ovary often with tan, brown, or red trichomes, and clusters of short spines, but those of the floral tube often naked or nearly so, the lower floral tube and pericarpel of several species (e.g., *S. stellatus* and *S. treleasei*) more typically with light-colored bristles; floral tube well developed, 2.5–10 cm long above the ovary; perianth commonly wide spreading or reflexed at anthesis, the inner parts typically white, cream, pale pink, or lavendar changing to darker shades to purple red outside and on the floral tube, but rathbunias pink changing to terracotta red; stamens numerous to very numerous (largest flowers), often with very long filaments; style with multilobed stigma, up to 14 stigma lobes, generally exserted from the floral tube and stems when the perianth is spreading; nectary chamber open or partially enclosed by the bases of the filaments, extending nearly a third the length of the floral tube in machaerocerei; at anthesis, immature fruit globular, 1–3 cm thick, the wall often mucilaginous; red pigmentation absent completely or present only in the ovary wall and not in the pericarpel; locule spherical to ovoid, 5–10 mm wide and at least half the diameter of the ovary, with the funiculi often markedly branched. Fruit globular to ovoid, 3–9 cm thick, generally lacking trichomes but typically having small laminae and clusters of long spines at maturity, the spines deciduous in some species; pulp of mature fruit red, sweet, edible. Seeds either brown or blackish brown, dull, verrucose, with a large basal hilum or glossy black with very fine punctae, 1.5–3.0 mm long.

This diagnosis indicates that *Stenocereus* is a very diverse genus, with a broad range of floral designs. Few, if any, features clearly define this genus, except that the flowers have small scales on the pericarpel, a long floral tube, and edible, ovoid to globose fruits that are very spiny at or just before maturity.

OTHER PACHYCEREEAE

To date, chemical investigations of other Pachycereeae have found that glycosidic triterpenes either are absent or are present only in trace amounts. Lupeol, a sapogenin (aglycon), is found in *Lophocereus*, in which alkaloids are

particularly abundant. None of the species here assigned to *Backebergia*, *Carnegiea*, *Cephalocereus*, *Lophocereus*, *Mitrocereus*, *Neobuxbaumia*, *Pachycereus*, and *Pterocereus*, has special epidermal funicular pigment cells at anthesis. Instead, at anthesis the pericarpel is chlorophyllous, the ovary wall is greenish white to white, and the funiculi and ovules are white. Red pigmentation of the fruit appears very late in development when a water-soluble betalain first is produced within the fruit wall and then occurs in the locule. Certain species have white pulp in ripe fruits, and green-fruited species occur in *Neobuxbaumia*.

Lophocereus.—2 spp. (Backeberg, 1960; Buxbaum, 1970b; Lindsay, 1963; Shreve & Wiggins, 1964). Flowers borne at shoot tips where flowering areoles become highly branched and produce long, gray white bristles, nocturnal, 2.5–4 cm long, broadly funnelform and nearly as wide as long when fully open; ovary and floral tube with very low podaria with small laminae but no conspicuous trichomes or spines; floral tube short, generally less than 1.5 cm long above the ovary; perianth widely spreading or rotate, the inner parts white to light or dark pink (*L. schottii*) or burnt coral (*L. gatesii*); stamens relatively few; style with 5–6 white stigma lobes, slightly exserted beyond the stamens; nectary chamber small and essentially open; at anthesis, immature fruit oblong, less than 1 cm thick, with a few scattered mucilage cells in the wall; locule oblong, to 6 mm wide. Fruit globular to oblong, 1–3 cm thick, glabrous, nearly spineless, with persistent laminae, bursting irregularly; pulp red and juicy. Seeds glossy, black, with a prominent raphe and a swollen collar around the hilum, 2 mm long.

Pachycereus.—6 spp. (Backeberg, 1960; Bravo, 1937, 1956a, 1956b; Britton & Rose, 1920; Buxbaum, 1963a, 1963b; Shreve & Wiggins, 1964). Flowers borne at shoot tips in most species but far down the ribs in *P. marginatus* and on old areoles in *P. weberi*, 1 per areole, except in *P. marginatus* which may have 2 per areole, diurnal or nocturnal, 4–12 cm long, broadly cylindric, cylindric-funnelform, or funnelform; ovary and floral tube covered by numerous, relatively low podaria, with small to medium-sized laminae, the areoles with tufts of tan, beige, or golden trichomes, particularly in *P. grandis*, *P. pecten-aboriginum*, and *P. pringlei*, with small light-colored bristles on the pericarpel and floral tube in *P. grandis*, *P. hollianus*, and *P. pecten-aboriginum*, present but inconspicuous only on the floral tube of *P. marginatus* and *P. weberi*, and essentially absent in *P. pringlei*; floral tube thickened, about half as long as the flower; perianth generally short, the parts spreading very far from the tube except in *P. weberi*, the parts white or ivory white in most species but sometimes rose in *P. marginatus* and purplish in the outer parts of *P. pecten-aboriginum*, minutely serrulate along the upper margins in several species; stamens numerous, particularly in large flowers; style with numerous stigma lobes, exserted above the level of the stamens except in *P. marginatus* and *P. weberi*; nectary chamber open or nearly so; at anthesis, immature fruit globular, 1–2 cm thick, seemingly wider in species with copious tan to golden trichomes that cover the pericarpel as a thick carpet, the wall thick and nonmucilaginous; red pigmentation absent; locule spherical, shieldlike (*P. hollianus*), or squarish (*P. marginatus*); ovules and funiculi generally not filling the locule, and in *P. pringlei* each branched funiculus with its numerous ovules widely spaced and discrete. Fruit globular or ovoid, 4–8

cm thick, burlike with long golden spines or bristles and trichomes (*P. grandis*, *P. pecten-aboriginum*, and *P. pringlei*), covered with abundant clusters of golden spines that are deciduous at maturity, or with fewer clusters of shorter, thinner spines or bristles and light-colored trichomes; pulp eventually red, burlike fruits generally dry and open by apical splits; fleshy fruits not very mucilaginous. Seeds mostly glossy black, comparatively large, 2–4.5 cm long, the raphe prominent in all species but especially in *P. hollianus* and *P. marginatus*; hilum typically oblique, with a thick collar in *P. marginatus*; testa thin.

Like *Stenocereus*, *Pachycereus* is a genus with diverse reproductive features. *Pachycereus marginatus* has small, tubular, white or rose-colored flowers, with some trichomes and virtually no bristles, small lightly armed fruits, and large seeds. *Pachycereus hollianus*, the type species of *Lemaireocereus*, has broadly cylindric flowers 7–10 cm long, with a short ivory white perianth, having conspicuous tufts of trichomes and numerous bristles, large ovoid fruits with numerous bristles, large ovoid fruits with numerous bristles, large ovoid fruits with numerous light-colored trichomes, bristles, and spines, and black shiny seeds with a prominent raphe. Flowers of *P. weberi* are funnelform, 8–10 cm long, with small tufts of coffee brown trichomes; the fruits are large, oblong, and naked at maturity because spine clusters are deciduous, and the seeds are large, black, and shiny without a prominent raphe. The remaining species have large cylindric-funnelform flowers covered with copious tannish trichomes, burlike fruits (less so in *P. pringlei*), and very large, black, shiny seeds with a small raphe.

Backebergia.—1 sp. (Bravo, 1961; Buxbaum, 1975b). Flowers produced within a dense terminal head of golden spines and bristles, 1 per aerole, nocturnal, 6–7 cm long, tubular; ovary and floral tube with podaria having fairly conspicuous laminae, conspicuous tufts of long tannish brown trichomes, especially on the pericarpel, and 1–several golden bristles per areole, especially on the floral tube; floral tube 3 cm long, relatively thick; perianth parts golden green, relatively short, mostly erect; stamens relatively few; style short with relatively few short stigma lobes, included; nectary chamber large but open, with a slight apical constriction; at anthesis, immature fruit 1.5 cm thick; red pigmentation completely absent, the walls green; locule semicircular in outline, with a small apical point, ca. 9 mm wide; ovules and funiculi not filling the locule. Fruit ovoid, 3.5 cm thick, covered by long trichomes and long mostly erect bristles; splitting irregularly, pulp wine red, juicy. Seeds shiny, black, 5 mm long, ca. 4 mm thick, with a prominent raphe and thin testa.

Mitrocereus.—1 sp. (Backeberg, 1960; Britton & Rose, 1920; Buxbaum, 1953, 1971a; Hertrich, 1934). Flowers borne at shoot tips, 1 per areole, the flower often subtended by long trichomes and bristles, nocturnal but remaining open the next day, 7–8 cm long, broadly cylindric-funnelform; ovary and floral tube with podaria bearing large leaflike laminae, but these hidden by copious, long tannish brown trichomes and some light-colored bristles; floral tube ca. 5 cm long, very thick; perianth parts rose red but when spreading cream-colored in the center; stamens numerous; style long, thick, with few very short stigma lobes, long exserted beyond the stamens and perianth; nectary chamber very large, well hidden by enlargement of the bases of the lowermost stamens; at anthesis, im-

mature fruit 2.5 cm thick, the walls with numerous, well-spaced mucilage cells; red pigmentation completely absent, the walls green; locule semicircular in outline with a small apical point, ca. 10 mm wide; ovules and funiculi not filling the locule, the funiculi often with papillate epidermal cells near the ovules. Fruit obovoid, greenish, 4 cm thick, lanate, with some bristles; pericarp mucilaginous, splitting lengthwise into 8 or more segments; plup white, relatively dry. Seeds shiny, black, larger than but similar in structure to those of *Pachycereus hollianus*, having a prominent raphe.

Cephalocereus.—20–30 spp. (Backeberg, 1960; Bravo, 1937; Bravo & MacDougall, 1959, 1963; Britton & Rose, 1920; Buxbaum, 1962a, 1971b; Marshall & Bock, 1941). Flowers borne near shoot tips, often in dense clusters, 1 per areole, nocturnal or diurnal, generally 3–8 cm long, but longer when the ovary is elongate, e.g., in *C. russelianus* (possibly not a member of this genus), funnelform or funnelform-campanulate, the flowering areole typically with numerous long soft white trichomes; ovary and floral tube often without prominent podaria but generally with noticeable laminae, especially in species referred to as *Neodawsonia*, the areoles sometimes with short trichomes but mostly lacking spines and bristles; floral tube often thickened and half as long as the flower; perianth parts generally spreading or reflexed, light pink to dark rose red; stamens numerous; style thickened, with up to 12 stigma lobes, commonly exserted slightly beyond the stamens; nectary chamber partially or completely closed; at anthesis, immature fruit globular or slightly flattened, but in certain species markedly oblong, rarely more than 2 cm thick, the wall thick and generally mucilaginous; red pigmentation absent, the walls green; locule mostly shieldlike or cordate in outline, with an apical point; funiculi with papillate epidermal cells in *C. hoppenstedtii* and *C. senilis*. Fruit usually depressed-globular, sometimes oblong, to 5 cm thick, completely naked, with small laminae only, or, in a few species, with small trichomes and spines; pericarp usually mucilaginous; pulp generally red, except in *Neodawsonia*, where sometimes white. Seeds poorly described, shiny, black or black brown, with very fine sculpturing, small.

Neobuxbaumia.—6 spp. (Backeberg, 1960; Bravo et al., 1970, 1971a, 1971b, 1973; Buxbaum, 1957; Dawson, 1952; Poindexter, 1949; Scheinvar & Bravo, 1973; Vail, 1960). Flowers borne mostly at shoot tips but produced on old areoles in *N. polylopha*, 1 per areole, nocturnal, 4.5–7.5 cm long, funnelform to funnelform-campanulate; ovary and floral tube with relatively large podaria and small to medium laminae, the trichomes and bristles usually inconspicuous or absent at anthesis, the podaria specialized as extrafloral nectaries at least in *N. polylopha*; floral tube relatively long and thick; perianth generally spreading, whitish to purple red; stamens numerous; style often with relatively few stigma lobes, included; nectary chamber typically large and closed for species where descriptions are available; at anthesis, immature fruit globular to ovoid-pyriform, 1–2 cm thick, the wall thick and mucilaginous, especially in the pericarpel; red pigmentation absent in the wall; locule either shieldlike or oblong, less than 1 cm wide; ovules and funiculi generally absent from the center of the locule, as in *Pachycereus pringlei*. Fruit globular to ovoid-pyriform, often with a persistent floral tube, rarely more than 4 cm thick, the podaria greenish, generally con-

spicuous but laminae may be absent, with some white trichomes and thin spines in some species, e.g., *N. mezcalaensis* and *N. tetetzo*, dehiscent but with 1–several apical splits; pulp generally dry, white. Seeds shiny, dark brown or black, with very fine sculpturing, obliquely reniform, up to 2 mm long.

Carnegiea.—1 sp. (Backeberg, 1960; Benson, 1969a; Bravo, 1937; Buxbaum, 1958b; Shreve & Wiggins, 1964). Flowers borne at shoot tips, 1 per areole, nocturnal but remaining open the next day, 10–12 cm long, 5–6 cm wide, funnelform; ovary and floral tube covered by relatively large podaria with conspicuous laminae, the areoles with whitish trichomes on the pericarpel and lower floral tube; floral tube 6–7 cm long, green, fused to the base of the style above the ovary for 1 cm; perianth commonly reflexed at anthesis, the inner and outer parts pure white; stamens extremely numerous, the filaments long and white; style with about 10 stigma lobes, exserted beyond the stamens; nectary chamber small and open, above point of fusion of style and floral tube; at anthesis, immature fruit globular to oblong, 1.5–2 cm thick, the walls with abundant mucilage cells; red pigmentation completely absent, the walls green; locule markedly oblong, 6–8 mm wide, packed with ovules. Fruit obovoid to ellipsoid, green tinged with red, 5–7 cm long, to 5 cm thick, with tufts of white trichomes and inconspicuous white bristlelike spines; pericarp mucilaginous, splitting lengthwise along 3 lines; pulp red. Seeds shiny, black tinged with red, the sculpturing merely slightly bulging epidermal walls, 1.5 mm long; testa relatively thin.

Anisocereus.—7 sp. (Backeberg, 1960; Buxbaum, 1970a).[5] Flowers 1 per areole, 7 cm long, cylindric-funnelform; ovary and floral tube covered with conspicuous green laminae, those of the pericarpel and lower floral tube subtending aeroles with trichomes and thin spines; floral tube 5 cm long, relatively thick; perianth parts orange red, relatively short, spreading; stamens numerous; style with relatively few stigma lobes, slightly exserted beyond the stamens; nectary chamber with a slight apical constriction but mostly open; at anthesis, immature fruit 1.5 cm thick; locule relatively wide. Fruit almost dry; pulp whitish. Seeds shiny, black brown, 3 mm long.

Pterocereus.—1 sp. (Backeberg, 1960; Glass & Foster, 1973; MacDougall & Miranda, 1954).[5] Flowers often borne on old areoles, 1 per areole, nocturnal with fetid odor, 8–9 cm long, cylindric; ovary and floral tube covered by podaria with large imbricated, recurved, green leaflike laminae, trichomes, and spines; floral tube 4.5 cm long, relatively thick; perianth parts numerous, yellowish green, strongly spreading or recurved at anthesis; stamens numerous; style with several short stigma lobes, approximately at the upper level of the uppermost stamens; nectary chamber fairly large and closed; at anthesis, immature fruit globular, 2.5–3 cm thick, the wall thick and lacking mucilage; red pigmentation absent, the walls green; locule shieldlike, 8 mm wide. Fruit becoming dry, 3–4 cm thick.

POLLEN GRAINS OF PACHYCEREEAE

As summarized by Leuenberger (1976), all Pachycereeae examined to date have very similar pollen grains, having the following features. *Size*: maximum

[5] Existing descriptions are very incomplete.

diameters 79–47 μm; minimum diameters 73–41 μm. *Structure and sculpture of exine*: tectate-perforate; finely anulopunctate; columellae 0.6–1.0 μm high, irregularly dispersed or reticuloid and numerous, 40–80 per 50 μm^2; spinules 2.5–0.8 μm high, isolateral or slightly concave. *Apertures*: almost exclusively tricolpate with occasional hexacolpate grains in tricolpate samples. Although Leuenberger does not advocate use of pollen data for classification of species within Pachycereeae, certain patterns do appear in his tables: (1) pollen grains of the two species of *Polaskia* are perfectly spherical and very similar to each other; (2) pollen grains of *Escontria* and *Myrtillocactus* are strikingly similar in exine features; (3) pollen grains of *Stenocereus* resemble those of *Polaskia* but are slightly larger and have fewer spinules and higher columellae; (4) pollen grains of S. *gummosus* very closely resemble those of S. *stelatus*; and (5) pollen grains of all species that lack stem triterpenes are very similar, being most similar to those of *Polaskia* among the triterpene-bearing species. The most divergent pollen grains in the tribe are those of *Lophocereus*, which have the tallest spinules and widest perforations.

SPECIES OF OTHER TRIBES OF CACTOIDEAE

Because most species of other tribes of columnar cacti are not included in this study, there is no need to summarize the reproductive features for species examined outside tribe Pachycereeae.

Most species have flower, fruit, seed, and pollen characteristics that closely overlap patterns in Pachycereeae. The seeds and pollen grains, as well as flower and fruit structure, of *Bergerocactus emoryi* (Benson, 1969a, 1969b; Moran, 1965; Shreve & Wiggins, 1964) indicate that this species is closely related to, if not derived from, tribe Pachycereeae and not Echinocereeae but also may represent a connection between Pachycereeae and Echinocereeae. *Bergerocactus* and *Echinocereus* lack pearl cells at anthesis (Buxbaum, 1975). In tribe Cacteae reproductive features of the genera with primitive features, e.g., *Echinocactus* and *Ferocactus*, are not unlike those of *Polaskia* and *Pachycereus hollianus*, which co-occur with these same species. Even though external features of flowers of *Machaerocereus* are superficially similar to those of Hylocereeae and Trichocereeae, other features of flowers, fruits, and seeds show that these taxa are not closely related (Buxbaum, 1968b). Tribe Cereeae has flowers and pollen grains similar to those found in Pachycereeae; however, phylogenetic reconstructions of the tribe (Buxbaum, 1968a, 1968c, 1968d; Leuenberger, 1976, after Buxbaum) clearly show that the species with flower and fruit characteristics similar to Pachycereeae, e.g., *Cephalocereus*, are the most highly derived phylads of the tribe, a result of convergent evolution. Although none of the genera of Leptocereeae and Browningeae are adequately described, published illustrations of their flowers (Buxbaum, 1963e, 1965, 1966; Rauh, 1958) are strikingly similar to flowers of *Polaskia* and *Pachycereus*, especially flowers of *Armatocereus* and *Samaipaticereus* (Leptocereeae), and *Browningia* and *Castellanosia* (Browningeae) of northwestern South America; in fact, species of *Armatocereus* were originally included in *Lemaireocereus* by Britton & Rose (1920).

Pollination

Few data are published on pollination of Mexican columnar cacti, and accounts often emphasize bat pollination (Alcorn et al., 1959, 1961, 1962; Howell, 1972; McGregor et al., 1959, 1962; Moran, 1962b; Porsch, 1939; Vogel, 1968). Bat pollination is probably very widespread in Pachycereeae in that many species are ideally suited for bat visitation. Their flowers typically open at night; are mechanically strengthened, funnelform-campanulate to campanulate; and have great numbers of anthers, a large stigmatic surface, and large, basal and hidden nectary chamber. The flowers are positioned near the tips of the branches, often held above the neighboring vegetation, and flower color is often white or light rose. In addition, some species also have strong fetid nocturnal odors, e.g., *Pterocereus gaumeri* (Glass & Foster, 1973), which has yellow green flowers covered with large leafy primordia. Flowers that are campanulate and open during the day may attract bird and insect visitors (Moran, 1961).

Flowers adapted for hummingbird visitation, including those of *Myrtillocactus*, *Pachycereus marginatus* (Beutelspacher & Martínez, 1973), *Polaskia chende*, *Stenocereus alamosensis*, S. *beneckei*, and S. *stellatus*, have diurnal anthesis, a pinkish to red short narrow floral tube and perianth parts, and an open nectary chamber; and in *Myrtillocactus*, *Pachycereus marginatus*, and S. *alamosensis* flowers are produced on old areoles along the stem rather than clustered at the tips. Hummingbirds have been observed visiting native populations of *Myrtillocactus cochal*, *M. geometrizans*, and S. *alamosensis*.

Although hawkmoth pollination has not been observed in Pachycereeae, we suspect that the long salverform pinkish flowers of machaerocerei, the narrow tubular pinkish flowers of *Stenocereus standleyi*, and the short tubular, rotate pinkish flowers of *Lophocereus*, which all open at night, are preferred by hawkmoths. Their nectary chambers are completely open.

Many species of cacti are visited by small insects foraging either on the copious pollen or nectar (e.g., Shreve & Wiggins, 1964), but the effectiveness of these small insects as cactus pollinators has rarely been measured (Alcorn et al., 1961; McGregor et al., 1959).

Closely related species often differ markedly in flower shape, length, color, and time of anthesis. For example, *Stenocereus alamosensis*, a northern desert species with diurnal flowers, and S. *standleyi*, a species of more mesic habitats with nocturnal flowers, are morphologically very similar; likewise *Lophocereus* with small clustered nocturnal flowers, *Pachycereus marginatus* with small tubular diurnal flowers, and *P. weberi* with funnelform nocturnal flowers are closely related to judge from all evidence of stem structure and chemistry. One may conclude from these and other examples that within Pachycereeae dependence upon relatively large, highly mobile animal vectors for outcrossed pollination has resulted in a radiation of floral designs. Therefore, differences between species that are pollination strategies in particular geographical regions must not be overweighed. Between geographically isolated species, one should expect to find not only differences in flower size, shape, position, color, and time of opening but also differences in the type and size of appendages on the exterior of the flower, e.g., to attract certain types of pollinators or to prevent injury

(spination) to animal vectors. The degree of development of primordia at anthesis, which is stressed in the classification of Britton & Rose (1920), may not be valid for delimiting genera.

Discussion

Comparative anatomy is useful in reconstructing phylogenies but is not automatically reliable by itself since internal tissues, like external structures, experience convergent and parallel evolution. Anatomical features are not necessarily conservative, because characters that affect the fitness of a plant are likely to be acted on by natural selection. Therefore, any worker is pleased to uncover sets of anatomical and other taxonomic features in otherwise similar taxa that are so unusual for flowering plants that the combination of features can clearly define a natural group (Thorne, 1958, 1963). The sets of anatomical, morphological, and biochemical features discussed above not only clarify the limits of subtribes within Pachycereeae but also help determine with reasonable certainty where dichotomies have occurred between related phylads and species pairs.

One natural group of Mexican columnar cacti has become clearly defined through observations in this study. Subtribe Stenocereinae (sensu Buxbaum) first included only *Stenocereus* (i.e., all species of *Lemaireocereus* except *L. hollianus*), *Carnegiea*, and *Lophocereus*; but later *Machaerocereus* and *Rathbunia* from the tribe Echinocereeae (Buxbaum, 1968b, 1969, 1975c) and subtribe Cephalocereinae were added to form one large subtribe (Fig. 33). We propose to emend and redefine this subtribe to include instead the taxa that have: (1) abundant stem triterpenes and no alkaloids (Table 1); (2) pigment cells in the epidermis of the funiculus in the flower; (3) generally small seeds (3 types); and (4) strong similarities in growth habit and vegetative and reproductive morphology and anatomy. Included here are all species that have silica bodies in the skin and the species of *Stenocereus* (s. l.) having areoles with red glandular trichomes. Many, but not all, species of *Lemaireocereus* (sensu Britton & Rose, 1920) are included here, as well as the genera *Escontria*, *Machaerocereus*, *Myrtillocactus*, and *Rathbunia*. We have in effect combined some members of all four subtribes of Buxbaum into one and have excluded *Carnegiea*, *Lophocereus*, and the Cephalocereinae, which have biochemical or morphological features more typical of a different subtribe. Because features such as presence of stem triterpenes, skin silica bodies, special funicular pigment cells, and areoles with red trichomes are apparently unlinked in any biological functions, their consistent occurrence together denotes monophyly: it is highly unlikely that this unique set of features, absent from other Cactaceae, has evolved more than once.

Within subtribe Stenocereinae two groups of genera are identifiable, those without and those with skin silica bodies. The first group consists of *Escontria*, *Myrtillocactus*, and *Polaskia*, the seven species with the smallest seeds in the tribe. All five records of chichipegenin (Table 1) occur in *Myrtillocactus* and *Polaskia*, and five species from all three genera have longispinogenin. These taxa are all trees 4–7 m tall with a distinct trunk to 1 m high; *M. cochal* tends to have the flattest crown. In addition, all species have relatively small flowers, and

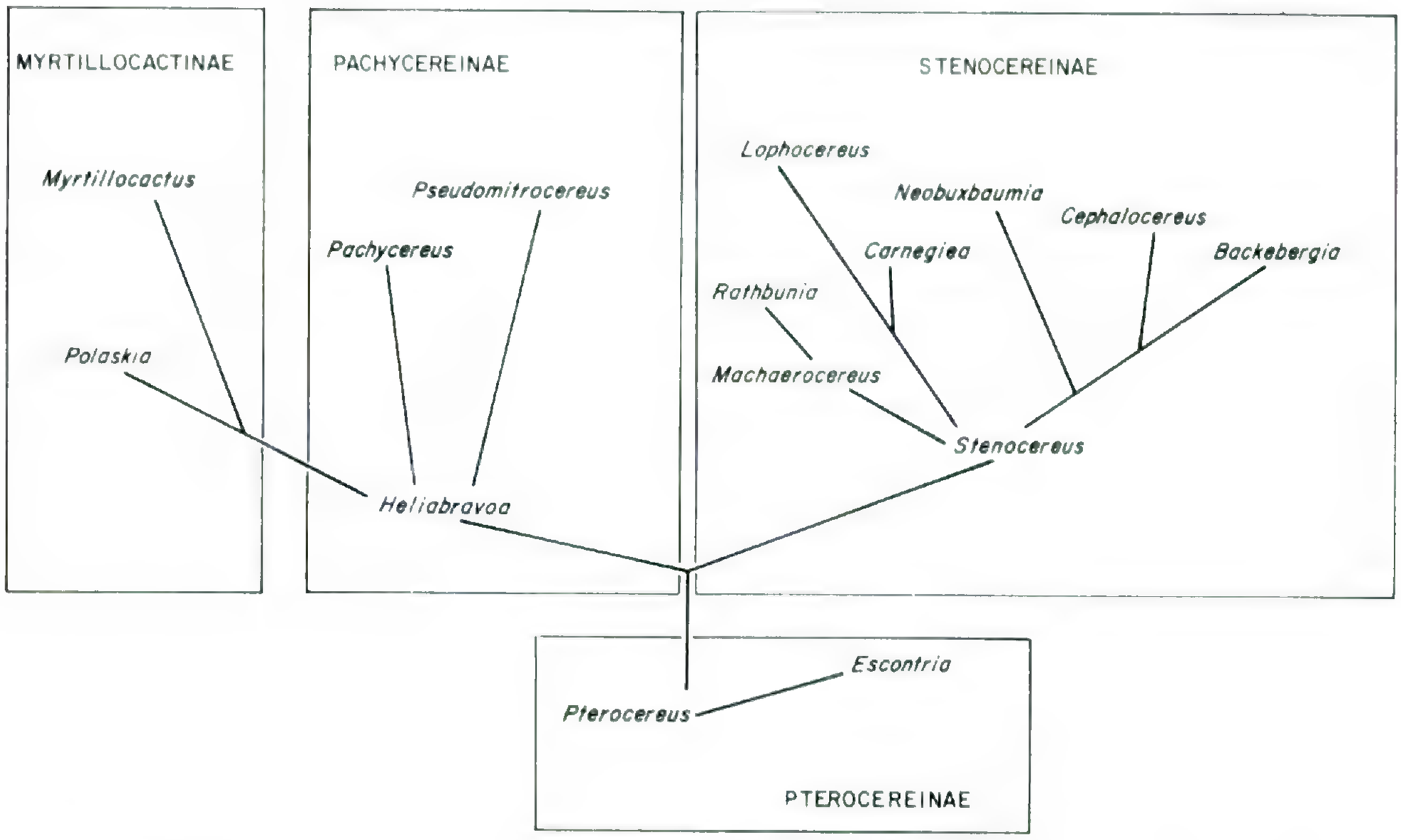


FIGURE 33. Approximate phylogenetic relationships of Pachycereeae according to Buxbaum (after Leuenberger, 1976).

pigmentation in the female part of the flower is restricted to the pericarpel and does not occur on the sides of or below the locule. The two species of *Polaskia* are obviously closely related to each other in the following ways: (1) stems light, bright green, a color uncommon in this tribe; (2) the sharply acute ribs bear morphologically similar areoles and spines; (3) rib number similar but generally higher in *P. chichipe*; (4) skin very thin, with a smooth cuticle, bullate multiple epidermis, and 1(–2)-layered hypodermis with lamellar primary thickenings; (5) cortex and pith lacking mucilage and crystal cells, and pith very narrow and lacking abundant starch; (6) external and internal structures of the flowers similar even though the number of primordia and trichomes on the pericarpel and short floral tube differ; (7) seed size and shape and testal surface features nearly identical; (8) pollen grains very similar, more so to each other than to other species of Pachycereeae; and (9) stem triterpenes very similar and biochemically very simple. *Escontria* and *Myrtillocactus* also show close relationships to each other in the following respects: (1) horns present on the outer epidermal walls, and these covered by a thick, rough cuticle; (2) hypodermis thick and lacking crystals; (3) mucilage cell patterns of the cortex and pith nearly identical; (4) both species with relatively narrow pith; (5) testal surface features of seeds strikingly similar; and (6) pollen grains nearly identical. Flowers of *Myrtillocactus* more closely resemble flowers of *Polaskia chende* than those of *Escontria* and may be viewed as very small versions of the former with almost no development of pericarpel vesture and armature and with stronger development of mucilage of the fruit. Nevertheless, *Myrtillocactus* is unusual because more than one flower occurs per areole, an uncommon feature in Pachycereeae found elsewhere in *Lophocereus*. Buxbaum (1962c, 1963d, 1967) has

repeatedly noted the relatedness of *P. chende* (as *Heliabravoa*), *Myrtillocactus*, and *Polaskia* for some of the reasons cited above, but he (1970) has compared *E. chiotilla* with *Pterocereus* and *Anisocereus*.

Stenocereus is a monophyletic taxon in which vegetative and reproductive features have undergone extensive evolution. All species studied here have silica bodies in the skin and highly mucilaginous stem cortex, but within the genus the distributional patterns and shapes of these features reveal smaller lines of radiation, paralleled by patterns observed in distribution of stem triterpenes.

Stenocereus stellatus and *S. treleasei*, species of southern Mexico, are the only known taxa to produce both stellatogenin and thurberogenin in the stem. Cactus taxonomists have consistently placed these species next to each other from similarities in growth habit, flowers, and fruits (Backeberg, 1960; Bravo, 1937); in fact, Backeberg includes only these species in *Stenocereus*. *Stenocereus treleasei* has a higher rib number than *S. stellatus*, fewer central and radial spines, and shorter flowers, with larger tufts of trichomes. This study also shows that their stem anatomy is nearly identical, especially the structure of the skin, in which the large silica bodies are found only in the hypodermis. The flowers of both species are similar in areolar features to *Polaskia chende* and in floral design to *Pachycereus marginatus*.

Stenocereus pruinosus is certainly closely related to the *stellatus* group to judge from superficial similarities in growth habit, stem anatomy, and seeds; but *S. pruinosus* is clearly distinct chemically and has longer, more funnelform flowers and has fruits with tan-felted areoles and numerous persistent yellow spine clusters. The general features of the shoot, especially those of the areoles, flowers, and fruits are also characteristic of *S. chrysocarpus* (Sánchez Mejorada, 1972), which has longer flowers and larger fruits. That species, however, has red glandular trichomes in the areoles in addition to the normal tan ones, and in this way is similar to *S. queretaroensis*. Studies of the stem anatomy and chemistry of *S. chrysocarpus* are needed to evaluate its relationships.

Another phylad within *Stenocereus* consists of *S. griseus*, *S. hystrix*, and *S. longispinus*, which have similar external features of stems and reproductive structures and also similar sets of unusual stem triterpenes (Table 1). *Stenocereus laevigatus* may also belong to this phylad, but its anatomy and chemistry are still unknown. Stem anatomy of *S. hystrix* and *S. longispinus* shows that this phylad belongs in the genus because silica bodies are present, and the seeds of this phylad are very similar to those of *S. pruinosus* and *S. stellatus*. The species are native to the West Indies, Guatemala, and southernmost Mexico, and in all likelihood this phylad is an early radiation from Mexican stock. The flowers appear to be adapted for nocturnal pollination by bats, which are particularly common in the ranges of these species.

Stenocereus dumortieri, which has been called *Isolatocereus dumortieri* (Backeberg, 1960), is certainly a highly specialized species of the genus and the largest species related to *S. pruinosus* and *S. chrysocarpus*. Ribs are few, bluish green or glaucous, and bear areoles that are very closely spaced. Spines are thinner than in most stenocerei, and the cortex is bright yellow, more so than in *S. pruinosus*. Moreover, *S. dumortieri* has a unique oleanane triterpene, dumorti-

erigenin, an unusual lactone compound that is probably derived biochemically from oleanolic acid. The flowers and fruits are most similar to those of the *stellatus* group, and their seeds also resemble those of S. *stellatus*, S. *hystrix*, and S. *pruinosus*. From these data, S. *dumortieri* appears most closely related to S. *pruinosus*.

Stenocereus beneckei, S. *martinezii*, S. *montanus*, S. *queretaroensis*, S. *quevedonis*, and S. *thurberi* appear to represent a phylad that has speciated in Mexico in Neuva Galicia and west of the Sierra Madre Occidental. All these species have red trichomes in stem areoles, and of the five species that have been chemically studied, four have queretaroic acid, a triterpene found in no other cacti. *Stenocereus martinezii*, which has never been studied chemically or critically described, is so similar to S. *thurberi* that their relationship is inescapable. All these species have similar external rib features, e.g., strongly sinuate margins, and S. *montanus* and S. *queretaroensis* have similar stem anatomy. *Stenocereus thurberi* has stem chemistry and skin silica bodies most similar to S. *stellatus*; however, its flowers and seeds are unlike those of S. *stellatus*, and the large mucilage sacs in the outer cortex are distinctive among columnar cacti examined, though other species from Sinaloa may share this feature. *Stenocereus queretaroensis* is closest to S. *stellatus* in vegetative anatomy and morphology but differs in having funnelform flowers. The seeds have not been described. Diurnal and nocturnal flowers occur in this phylad, and flower shape, length, and color are also variable, presumably in response to natural selection for preferred pollinators.

The recently described *Stenocereus fricii* (Sánchez Mejorada, 1973a) is difficult to compare to other stenocerei because no chemical and anatomical data are available. The growth habit most closely resembles that of S. *stellatus* and the previous phylad with red glandular trichomes, e.g., S. *montanus* and S. *quevedonis*. However, S. *fricii* has cream-colored felt on the areoles and has flowers and fruits similar to those of S. *pruinosus* and S. *chrysocarpus*.

When Britton & Rose (1909) established the genus *Rathbunia*, several species of *Stenocereus*, then *Lemaireocereus*, had not been yet described, including species from Sinaloa and Nueva Galicia. Consequently, the conspicuous red tubular flowers of *Rathbunia* were quite distinctive from typical funnelform flowers in *Lemaireocereus*. When *L. standleyi* was described from Sinaloa, the distinctions between these genera were diminished. This species has strongly sinuate rib margins that bear well-developed clusters of numerous radial and central spines in areoles that generally lack trichomes. Comparisons of S. *standleyi* with rathbunias show very few differences, either superficially or anatomically; rathbunias appear to have fewer and smaller silica bodies. Flowers and fruits of these taxa are closely similar even though the flowers of S. *standleyi* are lighter in color, more funnelform, and nocturnal, whereas those of rathbunias are red, tubular, and diurnal. In addition seeds of both are about 2 mm long, shiny, and black, with minute punctae, a seed type uncommon in Stenocereinae. All these observations support a conclusion that *standleyi*, *alamosensis*, and *kerberi* belong in the same genus, the principal difference in the flowers having arisen by adaptation to different pollinators. *Rathbunia* thus must be transferred to *Steno-*

cereus. More study is needed of these northern species of *Stenocereus*, especially the morphs of S. *standleyi*, to determine to what other species they are related. Likely close relatives are S. *quevedonis* and S. *montanus*.

Even with information on stem anatomy and chemistry, placement of *Stenocereus deficiens* is difficult, and we prefer to remain uncommitted on this Caribbean species until the flowers and fruits are better described.

Machaerocereus is clearly related to *Stenocereus*, as seen by Britton & Rose (1909) when they placed the species in *Lemaireocereus* before establishing *Machaerocereus* (1920). Justification for this segregation was that the growth habit of *Machaerocereus* is more lax than in *Lemaireocereus*; spine clusters are well developed and bear a strongly flattened, downward-pointing central spine; and the perianth is very elongate and relatively long persistent. Although the triterpenes of each *Machaerocereus* species is different (Djerassi, 1957), these taxa have similar hypodermal silica bodies and seeds, and the flowers and fruits are quite similar, though the parts are darker colored in *gummosus*. On the basis of gross similarities in vegetative form, stem anatomy, triterpene chemistry, and seed structure, machaerocerei are more closely related to S. *stellatus* than to other cacti examined. However, S. *fricii* from Nueva Galicia, Mexico (Sánchez Mejorada, 1973a), also has several vegetative and reproductive similarities to *Machaerocereus*. Regardless whether machaerocerei are most closely related to S. *fricii* or S. *stellatus*, the morphological gap is not great enough to recognize *Machaerocereus*. Therefore, we recommend assigning *eruca* and *gummosus* to *Stenocereus*. The floral divergence of machaerocerei is, of course, overemphasized by the strong dependence of this phylad for nocturnal pollination by, presumably, hawkmoths.

Backeberg (1960) recognized seven genera for the species here included in *Stenocereus*, but none of the segregates is strongly defensible. Both *Marshallocereus* and *Ritterocereus* are artificial phylads, composed of species from several separate lines, and *Hertrichocereus*, *Isolatocereus*, *Machaerocereus*, and *Rathbunia* are extreme forms. For example, *Hertrichocereus* (=S. *beneckei*) has markedly glaucous stems, and *Isolatocereus* (=S. *dumortieri*) has flowers produced for long distances from shoot tips. Such segregates tend to confuse workers not familiar with cactus taxonomy and overemphasize differences between species, obscuring the fact that they are monophyletic. We support Buxbaum's (1963d) conclusion that such names are unnecessary and should not be used.

The genus *Pachycereus* has been difficult to circumbscribe since Britton & Rose (1909) first proposed it to include arborescent cacti with trichome-covered flowers and burlike fruits. Their treatment of *Pachycereus* in 1920 recognized ten species in a more broadly defined genus. Since 1920 various workers have shown that their genus was artificial; *P. orcuttii* is really an intergeneric hybrid between *P. pringlei* and *Bergerocactus emoryi* (McGill & Pinkava, 1974; Moran, 1962a, 1963); *P. columna-trajani* and *P. ruficeps* are synonyms of species belonging to other genera of Britton and Rose; and *P. chrysomallus* of Britton and Rose is the plant now recognized as *Mitrocereus fulviceps*, which was inadvertently included in synonymy of another distinctive species, now called *Backe-*

bergia militaris (Sánchez Mejorada, 1973b). Two other species have been removed from *Pachycereus* by most authors and assigned to *Pterocereus* or to *Pterocereus* and *Anisocereus* (Backeberg, 1960) or *Escontria* (Buxbaum, 1970a). *Lemaireocereus hollianus*, the type of its genus, has been transferred to *Pachycereus* by Buxbaum (1961), especially on seed characteristics, and *P. marginatus* has been transferred to *Lemaireocereus* (Berger, 1929) and to *Stenocereus* (Buxbaum, 1961). Another arborescent species, *L. weberi*, has been placed in *Pachycereus* by Backeberg (1960). Therefore, only three species, *P. grandis*, *P. pecten-aboriginum*, and *P. pringlei*, have consistently been retained in the genus.

Confusion on the generic limits of *Pachycereus* can be resolved only after the phylogenetic relationships of the species are clearly understood. The genus is composed of several divergent phylads; consequently, no set of taxonomic features satisfactorily defines the genus. Species appear to lack crystals in the skin, and they have stem alkaloids that form red and then black pigments after wounding. Moreover, all species have large black shiny seeds, generally with a conspicuous raphe. The two species that lack stem mucilage, *Pachycereus hollianus* and *P. marginatus*, also are the only species in the subtribe that have outer epidermal-cell horns, a feature found only in the other subtribe in *Myrtillocactus* and *Escontria*. Although this feature may have evolved convergently, it is more likely that it developed in parallel from a common ancestor. These two species of *Pachycereus* are not similar in vegetative morphology or anatomy, but the flowers are closely similar, having very short perianth parts that barely extend beyond the floral tube, and the floral tube and pericarpel have axillary tufts of tannish trichomes. Especially *P. hollianus* has prominent bristles at anthesis, the ones in *P. marginatus* appearing only on the floral tube. The mature growth form (Backeberg, 1960) and skin anatomy of *P. marginatus* resemble those in *P. weberi*, which is the most massive Mexican cactus. In this regard and in the presence of some mucilage cells in the cortex, *P. weberi* is more highly derived. The flowers of *P. weberi* are funnelform with a conspicuous white perianth, and with axillary tufts of tannish trichomes and bristles. Both *P. marginatus* and *P. weberi* bear flowers far down the ribs from the shoot tips, and the flowering areoles typically bear numerous gray white bristles, an uncommon feature in Pachycereeae, otherwise found only in *Lophocereus*. Stem anatomy of *P. weberi* is extremely similar to that of *P. pecten-aboriginum* and *P. pringlei*, but in *P. pringlei*, as in *P. grandis* and *P. pecten-aboriginum*, the flowers generally have conspicuous tufts of tan axillary trichomes. The latter two species have bristles at anthesis, which are generally lacking at anthesis in *P. pringlei*. The seeds are very large, black, and glossy in the four largest species of the genus; and in *P. grandis*, *P. pecten-aboriginum*, and *P. pringlei* the fruits are burlike, covered with golden trichomes and long stiff bristles. In both *P. marginatus* and *P. weberi* the trichomes and bristles are deciduous at maturity, but in *P. hollanius* both spines and bristles are retained at maturity.

Closely related to *Pachycereus*, in particular to *P. marginatus*, are the two species of *Lophocereus*, *L. gatesii*, and *L. schottii*. The growth habit of *L. schottii* can be obtained by shortening the base of a mature specimen of *P. marginatus*. All aspects of the external shoot morphology show the clear relation-

ships of these two genera. Flowers of *Lophocereus* differ from those of *Pachycereus marginatus* in being smaller, more numerous per areole, and adapted for nocturnal pollination, probably by hawkmoths, whereas flowers of *P. marginatus* are pollinated in the day by hummingbirds. The fruits of *Lophocereus* are almost spineless, yet the seeds within the red pulp are strikingly similar to those of *P. marginatus*. With all of these features in common, the occurrence of the same alkaloid in only these taxa is convincing proof of their relationship, even though the epidermis differs just as it differs between *Polaskia* and *Myrtillocactus*. Stems of *Lophocereus* do not blacken after wounding.

Backebergia militaris is tentatively recognized in this treatment as a distinct genus but has not been anatomically or biochemically studied. Strong similarities in growth habit, external shoot morphology, and flower and fruit structure (Bravo, 1961; Buxbaum, 1975b) between *B. militaris* and *Pachycereus* not only show a relationship but raise the question whether the species cannot be included in *Pachycereus*. The flowers and fruits have numerous long bristles and golden trichomes, but as in no other species of *Pachycereus*, the flowers are borne terminally within a dense crown of golden spines.

Pachycereus gaumeri and *P. lepidanthus* have been moved to other genera (see Glass & Foster, 1973) because the floral tube of each is covered with prominent leaflike scales. In *Pterocereus gaumeri*, the stems have three or four high, very acute ribs bearing widely spaced aeroles with a few short spines, and the stem has a thin, crystalless skin and a densely packed, nonmucilaginous cortex, similar to that of *Pachycereus marginatus* and *Polaskia*. In *Anisocereus lepidanthus*, the stems have seven to nine extremely low ribs, with closely spaced areoles and conspicuous thin spines, and the stem is nonmucilaginous but less compact, appearing more like stems of *Cephalocereus*. Moreover, *A. lepidanthus* has prismatic crystals in the skin. For these reasons we have chosen to segregate these species from *Pachycereus* and from each other as two genera, *Pterocereus* and *Anisocereus*. Though these species probably share some common ancestry, the gap between them is difficult to determine without adequate data on flowers, fruits, seeds, and stem chemistry. If they do belong to Pachycereeae, they certainly are older derivatives than any other extant genus. Buxbaum (1961) expressed the same point of view when establishing the primitive subtribe Pterocereinae to include these species. However, he made this decision because of leafy appendages on the floral tube, feeling that a leafy floral tube must be the primitive condition. On the contrary, there is no convincing evidence that the tribe arose from ancestors with floral tubes having very large leaves, and it is probable that increased leafiness is correlated with dependence on nocturnal pollination by bats, especially in *Pterocereus*, in which flowers are dull in color and produce fetid nocturnal odors (Glass & Foster, 1973).

Sorting out the relationships and phylogeny of the remaining species is not completely possible at this time because data on stem chemistry and stem anatomy are unavailable for most species. *Carnegiea gigantea* seems closely related to *Pachycereus* when chemical data are used but more closely related to *Neobuxbaumia* based on similarities in growth habit, vegetative morphology, and flower and fruit structure. Not surprisingly, several species of *Neobux-*

baumia have *Pachycereus* synonyms, and the only other species ever placed in *Carnegiea* was *N. euphorbioides*. *Carnegiea* has traditionally been considered a very isolated genus, unrelated to any sympatric species in the Sonoran Desert. Workers should have compared features in *C. gigantea* with those of *N. mezcalaensis* and *N. tetetzo*, whose vegetative and reproductive structures are remarkably similar to *Carnegiea* except that these species of *Neobuxbaumia* have slightly smaller flowers and fruits. On the mature fruits, both *C. gigantea* and *N. tetetzo* have a conspicuous ring of white trichomes at the base, small persistent tufts of white areolar trichomes, and a few, hardly noticeable whitish bristles. Moreover, seeds of *Carnegiea* and *Neobuxbaumia* are relatively small and glossy black to reddish black, and the testa is noticeably thin in comparison to those of other cactus seeds. *Neobuxbaumia polylopha* has most unusual reddish purple, strongly angular flowers with pronounced podaria that function as external nectaries. Certainly Dawson (1952) was correct in pointing out the closeness of *Carnegiea* and *Neobuxbaumia*.

Mitrocereus fulviceps resembles *Backebergia*, *Neobuxbaumia*, and *Pachycereus* in growth habit and rib features; and the stem anatomy is not unlike that of *Neobuxbaumia*, although *M. fulviceps* has fewer epidermal cells with crystals and great densities of crystal aggregates in the pith and cortex. However, the reproductive features of *Mitrocereus* show no close relationships to any single genus. The flowers are extremely wide and are similar in longisection to those of *Cephalocereus senilis*; but the pericarpel has copious shaggy trichomes and flexible golden bristles more typical of *Backebergia*. Fruits split open in the same fashion as *Carnegiea* and *Neobuxbaumia*, and the pulp is white and of the same consistency as in certain species of *Neobuxbaumia* but not *Carnegiea*. Seeds closely resemble those of *Backebergia* and *P. hollianus*. Based on these meager superficial comparisons, phylogenetic placement of *Mitrocereus* is most defensible between *Backebergia* and *Neobuxbaumia*, near the divergence of Mexican species of *Cephalocereus*.

Classification of species currently assigned to *Cephalocereus* and its numerous segregate genera is still a major unresolved systematic problem. As a single genus, in which species typically have unarmed flowers and fruits and flower-bearing areoles with long wooly trichomes, the type is *C. senilis*. This species is highly derived, with a solitary columnar arborescent growth habit and a large lateral pseudocephalium in which the flowers are produced. Observations in this study indicate that all eight species of cephalocerei, including the type and *C. hoppenstedtii*, its closest relative, but excluding *C. russelianus*, have numerous small prismatic calcium oxalate crystals in each epidermal cell, regardless of the features of the external shoot. This crystal pattern also occurs in *Neobuxbaumia* and, to a lesser degree, in *Mitrocereus*. We conclude that *Cephalocereus* should include those species of cephalocerei from mainland North America, the West Indies, and coastal northern South America that have this crystal pattern. We cannot determine whether *C. russelianus* and its relatives are a related South American phylad. Because most species of cephalocerei were not examined in this study, we cannot determine whether certain South American taxa, particu-

larly species in Brazil, belong to this tribe. Buxbaum (1958a, 1968d) has concluded that these species belong in tribe Cereeae and not in Pachycereeae.

Authors have the choice of emphasizing differences or similarities, with liberal or conservative schemes, respectively. We feel use of too many generic names confuses the reader by overstating the importance of small differences in cactus structure. In a very liberal classification of cactus genera one loses appreciation for the interrelationships of taxa by segregation without significantly improving their systematics. Conversely, use of a single genus, *Cereus*, for all columnar cacti obscures interesting evolutionary trends. Even though sufficient comparisons between North and South American species have not been presented here, it is clear that for Mexican species, gaps between phyletic lines, based on morphology, anatomy, and biochemistry, are as evident as between genera and subtribes in other plant families. A single genus for all columnar cacti is therefore not systematically justifiable, and we recommend the abandonment of the name *Cereus* for Mexican species.

Phylogeny of Mexican Pachycereeae

The most useful phylogeny of Pachycereeae has been that of Buxbaum (Fig. 33), who employs data on stem triterpenes, funicular pigments, and seed morphology to assign genera to the tribe. Evidence summarized here supports the following conclusions of Buxbaum: (1) *Polaskia chende* (syn. *Heliabravoa*), *P. chichipe*, and *Myrtillocactus* are closely related, and *P. chende* has retained many primitive features; (2) *P. chende* is closely related to *Stenocereus*, particularly S. *stellatus*, and *Pachycereus*, especially *P. hollianus*; (3) *Machaerocereus* is directly derived from *Stenocereus*; (4) species of *Stenocereus* from the West Indies and Central America are derived from southern Mexican taxa (Buxbaum, 1963b); and (5) *Anisocereus lepidanthus* (as *Escontria* in Buxbaum, 1970a), *Pachycereus marginatus*, *Pterocereus gaumeri*, and *Stenocereus stellatus* are all old taxa of the tribe. Buxbaum (1963b) has also concluded with ample justification that *Hertrichocereus*, *Marshallocereus*, and *Ritterocereus* of Backeberg (1960) are unnecessary segregates of *Stenocereus* because these genera are too narrowly defined. Data presented here do not support Buxbaum's placement of *Stenocereus beneckei* next to either *Pachycereus weberi* or *Lophocereus*; of *P. weberi* very close to *Carnegiea gigantea* (Buxbaum, 1963b); of *Pachycereus* as nearest neighbor to *Mitrocereus*; of *Stenocereus dumortieri* near *Pachycereus marginatus*; or of *P. weberi* and *P. marginatus* in *Stenocereus*. Moreover, *Escontria* seusu Buxbaum (1970a) is artificial, misinterpreted from similarities of primordia on the floral tube. Although Buxbaum has never emphasized presence of stem triterpenes and funicular pigment cells to construct subtribal phylogenies, in his diagram all of these genera are directly connected except *Escontria* (Fig. 33). According to his phylogeny, it follows that species lacking triterpenes have evolved from triterpene-bearing species numerous times.

In order to construct phylogenetic systems, authors must propose and justify what are the primitive features for the higher taxonomic subdivisions. Characters of nonsucculent species of *Pereskia* are presently regarded as primitive for cacti as a whole (Gibson, 1975), and if Pachycereeae are directly or indirectly related

to the pereskias, one must expect that relatively nonxeromorphic features are primitive for columnar cacti, i.e., very thin cuticle; little or no hypodermis; no mucilage structures in the cortex, pith, or flowers; few, if any, crystals; narrow pith; and highly lignified wood; and the stem would probably have few ribs because at some time in the past the line arose from cylindrical stems. The plants should have the growth habit of a "normal" small tree, as in *Pereskia*, and have few spines that are not strongly dimorphic. All these features sharply describe *Polaskia chende*, which we regard as the closest extant species to the ancestral stock. Interestingly, *P. chende* has a growth habit, flowers, and fruits that are intermediate in characters between *Stenocereus* in subtribe Stenocereinae and *Pachycereus* in Pachycereinae. Moreover, the triterpenes present in stems of *P. chende* are biochemically very simple in comparison to compounds found in the rest of the subtribe.

Any feature regarded as primitive may be secondarily derived in other species. The single evolutionary trend that appears to be unidirectional in Pachycereeae is the acquisition of abundant mucilage cells from nonmucilaginous forms. Based on intuitive reasoning, one expects that mucilage is so important to a succulent plant that, once attained, this feature with associated anatomical structures is difficult to eliminate through natural selection. Interestingly, the absence of stem mucilage in species of Pachycereeae is usually correlated with thin hypodermis, narrow pith, and relatively few ribs, but some species with thin hypodermis or few ribs are found to have abundant mucilage. Therefore, the character of mucilage cells probably is not directly linked to other morphological features, at least in columnar cacti.

When all the phylads described and justified in the previous sections are brought together and species which lack mucilage are placed near the base of a phylogenetic tree (Fig. 34), a great number of taxonomic problems may be resolved. For example, *Pachycereus hollianus*, *P. marginatus*, and *P. weberi* have been assigned in the past by various authors to *Lemaireocereus* or *Stenocereus*, and by their position one can see that they are, indeed, fairly closely related to *Stenocereus*. Similarities between growth habits of some taxa are observed between early phylads of the closely related subtribes, thus giving some justification for using growth habit in classification of these plants.

Evolutionary Trends of Features Within Pachycereeae

If the proposed phylogeny is accurate, the following points may be advanced to explain diversity of features within the tribe Pachycereeae.

1. Stem chemistry. The presence of abundant triterpenes and alkaloids in cacti has probably served throughout time to discourage foraging on succulent tissues by animals. Living specimens of columnar cacti of Mexico, even those with few spines, are generally not food plants for vertebrate predators (Kircher & Heed, 1970). Cactophilic species of *Drosophila* are found only in rotting parts of cacti, not in uninfected tissues. One may wonder whether secondary plant substances are in any way able to inhibit the growth of microorganisms, providing a defense primarily against bacteria and fungi. Unfortunately, sufficient data are not available to determine whether diversity of compounds is a response

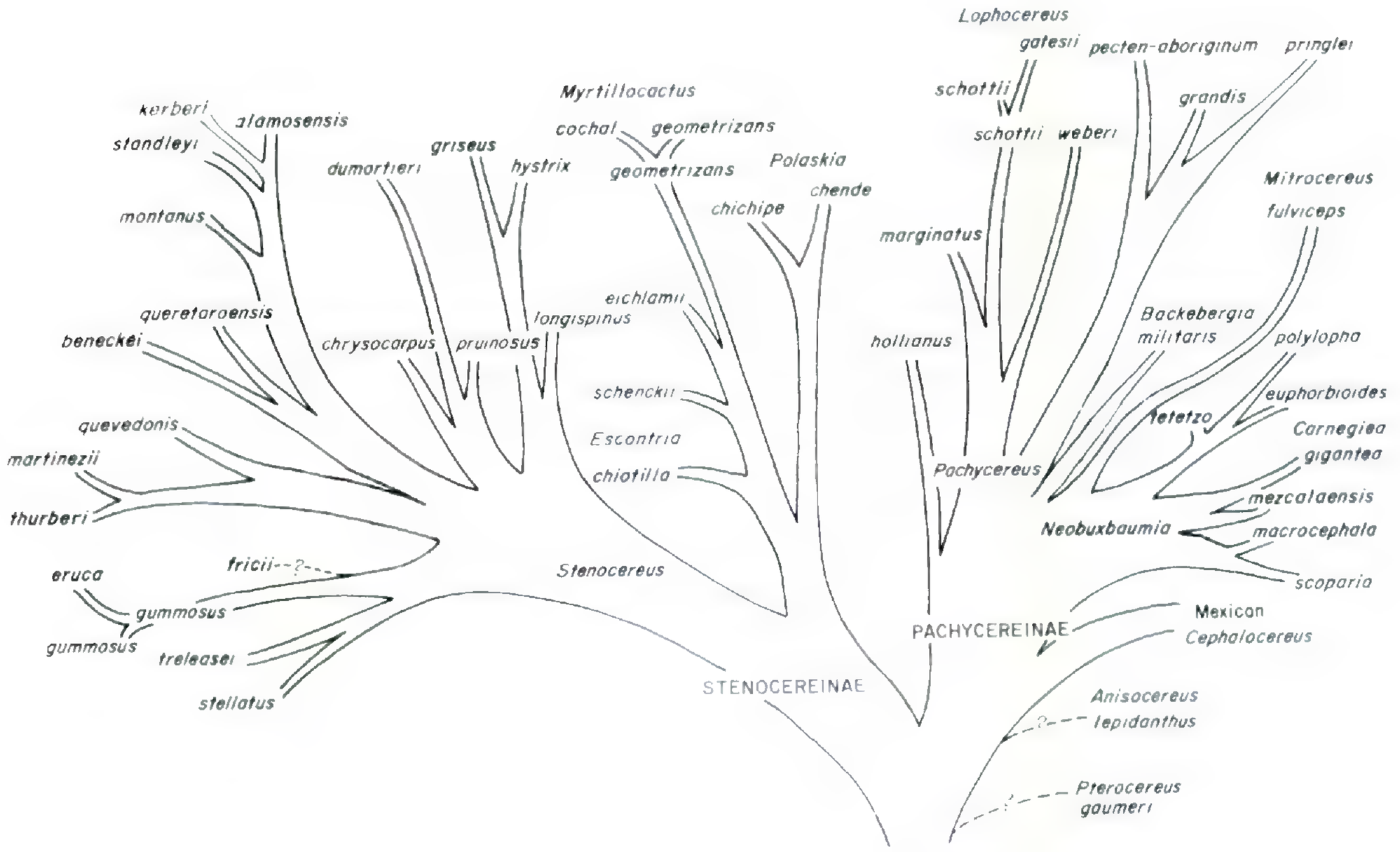


FIGURE 34. Proposed phylogeny of Mexican Pachycereeae (excluding poorly known species) based on current observations. Steps used in the construction of the phylogeny are those outlined by Throckmorton (1965) for *Drosophila*. In this phylogeny, primitive features are found closest to the center of the phylogenetic tree. Primary variables stressed in this phylogeny are stem chemistry, funiculus pigmentation, seed morphology, growth form, rib morphology and anatomy, and flower morphology.

through natural selection for better defense against microorganisms or insects. However, it is clear from other summaries on plant chemicals (Hegnauer, 1963, 1964, 1966) and Ponsinet et al. (1968) on cactoid Euphorbiaceae that triterpenes are particularly common in many stem and leaf succulent angiosperms, another example of convergent evolution of succulent plants. Presence of abundant alkaloids may be linked to rapid callus formation after wounding.

2. Growth habit and form. Tall tree species have evolved apparently in response to bat pollination in both subtribes, whereas shorter growth habits seem to have evolved for pollination by hummingbirds or hawkmoths. In Pachycereinae taller species have evolved through an increase in length of the trunk, an increase in the erectness and length of primary branches, and a decrease in the number of secondary branches. In Stenocereinae, some species have converged to arborescent forms with shorter trunks and narrower stems than arborescent Pachycereinae. Species shorter than their original stock have mostly arisen by a decrease in the length of the trunk and of primary branches.

Species with the primitive features tend to have relatively few, acute ribs, whereas more specialized growth habits tend to have rounded ribs that range in number from four to more than 50. This diversity is attributable to at least two major factors. Firstly, number of ribs is partially determined by the diameter of the stem, which is strongly correlated with plant height. Therefore, the

thicker the stem, the more ribs that are needed to cover the surface. This increase in rib number is certainly influenced by changes in phyllotactic patterns on the shoot apex. Secondly, rib number and stem thickness have been shown to be adaptations of plants to different geographical situations (Felger & Lowe, 1967). Populations of a single species vary widely in rib number, and those in the coldest (or highest latitudes) habitats tend to have the lowest surface-volume ratio to protect adult plants or seedlings against low winter temperatures. No one has tried to explain what determines the highest ratios in southernmost habitats. One cannot wholly discount that there may be advantages for carbon fixation and water conservation in certain growth forms or habits. Ribs do, of course, increase the photosynthetic area of the stem but at the same time decrease the amount of stem illuminated with direct sunlight because of the shadow effect. On the other hand, valleys between ribs may have thicker boundary layers and slightly cooler temperatures and, therefore, lower transpiration rates. Ribbing of the stem is important to accommodate diurnal (Schroeder, 1975) and seasonal (MacDougall & Spalding, 1910) expansion and contraction of the stem. Therefore, differences in rib number and stem thickness between closely related species may be a physiological response to different regional climates.

3. Spination of ribs. Length and strength of spines have generally increased in the highly specialized Pachycereeae; species with primitive features tend to have few, short spines.

4. Stem succulence and mucilage production. All species in the tribe have abundantly succulent stems, but there is also a trend for the increase in diameter and starch-storing ability of the pith. Moreover, within each subtribe mucilage production has evolved first in the cortex and then in the pith, with an overall increase in the amount in the main stem cortex and ribs. Especially in Pachycereinae, increase in size of pith is closely correlated with increase in plant height and total stem diameter.

5. Skin. On a broad scale, relative thickness of the cuticle is unreliable for predicting whether a species grows in an arid or semiarid habitat. Species with vastly different skin thicknesses are sympatric, e.g., in the Sonoran Desert; rather, trends in cuticle thickness appear to follow systematic lines. Sampling here is insufficient to determine evolutionary changes in cuticle thickness within phyletic lines or in different habitats for a single species, but in a study with adequate sampling (Conde, 1975), no trend in cuticle thickness was observed in populations of five species of *Opuntia*.

Glaucous stems have evolved convergently several times within Pachycereeae and numerous other times in other Cactoideae. Occurrence of glaucous stems is not correlated with specific habitats.

In several Pachycereeae, especially relatively old taxa, epidermal cells proliferate to form a minutely bullate surface. This feature is found at the base of our phylogenetic tree in both subtribes. Other early lines have horns on the outer epidermal walls, a feature not known in other Cactaceae.

Unlike other xerophytes, columnar cacti generally do not have sunken stomates. Only in several species are the stomates well below the level of other epidermal cells, particularly species with very thick cuticle. Pachycereeae are

probably CAM plants (not yet demonstrated) so that retaining stomates at the level of the stem surface may facilitate gaseous exchange during periods of nocturnal carbon fixation.

Thickness of the skin varies greatly within Pachycereeae and even within a single species. One clear evolutionary trend is an increase in thickness of the skin, especially the hypodermis, within each subtribe. However, species with vastly different thicknesses are often sympatric, suggesting that thickness alone is not an ecological adaptation. Skin is obviously important to deter predators, to conserve water, and to insulate the plant. Therefore, we would expect that certain physiological properties of the skin have also evolved in this tribe, e.g., the ability of protoplasts and proteins to withstand very high temperatures. One might also expect to find that the physiological ability of seedlings and mature plants to withstand coldest winter temperatures has evolved in the tribe.

Many species have crystals in the skin, probably as a mechanical deterrent to herbivores to increase the toughness and reduce the palatability of the skin. Because these crystals presumably arose millions of years ago, speculation as to the probable herbivores excluded is unwarranted. Crystals certainly can interfere with feeding of insects with chewing or sucking mouth parts. Diversity of patterns within phylads sheds no light on the probable functions of these crystals but does serve as a useful systematic tool.

6. External morphology and size of flower. As pointed out in a previous section, divergence in floral design is one of the most conspicuous evolutionary trends in Pachycereeae. These species seem to have depended on relatively large, highly mobile animal vectors for outcrossed pollination throughout their evolutionary history. The result has been a radiation of floral designs in each subtribe. In addition to visitation by small insects, members of this tribe are undoubtedly attractive to bats, hummingbirds, or hawkmoths.

Flowers of Pachycereeae with the primitive features are generally 4–5 cm long and have a relatively small ovary at anthesis. Flower size has generally increased in nearly all phylads with concomitant increases in numbers of anthers and stigma lobes and size of ovary and locule. Nevertheless, there are no unidirectional trends in the evolution of flowers, and development of features appropriate for one type of pollinator appears to have been opportunistic and not predetermined by the structure of the stock. Flowers of *Myrtillocactus* and *Lophocereus* certainly show a reduction from the primitive size, and these genera have also converged to produce more than one flower per areole.

7. Seeds. Seed size and testal morphology range widely within the tribe, but features are fairly constant within genera. The smallest seeds in each subtribe tend to occur in the species with other primitive features. Buxbaum (1955) has previously observed that seeds of this tribe lack perisperm and endosperm and that evolution of the embryo has been toward an increase in succulence of the hypocotyl-root axis and a reduction in size of the cotyledons. The increase in seed size is therefore related not only to attraction of bird dispersers for the seeds but also to an increase in embryo size which improves chances of seedling establishment. Fruits that split open at maturity are certainly adapted to attract

animals toward the dark colored seeds, some of which are very large, as in *Mitrocereus* and *Pachycereus*.

Evolutionary History of Pachycereeae

The probable center of origin of Mexican Pachycereeae appears to have been southern Mexico. Over half the Mexican Pachycereeae occur in Puebla and Oaxaca, and all the species whose stems lack mucilage cells and have a thin hypodermis occur in this same region and in neighboring states to the south. Moreover, the least specialized features of a genus or phylad occur near or in Puebla or Oaxaca, and the most specialized, such as the most mucilaginous stems, are farthest away. Lines of speciation radiate out from southern Mexico into northwestern mainland Mexico and Baja California and into the West Indies. For example, a group of species with red glandular areolar trichomes has evolved in Nueva Galicia and on the western side of the Sierra Madre Occidental. Therefore, the ten species of columnar cacti that occur in the Sonoran Desert are highly derived end products of a variety of phylads from the south, and the sympatric species are not closely related.

At least one author (Friedrich, 1974) has suggested that interspecific hybridization has been an important evolutionary factor in Cactaceae, but this is probably not the case for tribe Pachycereeae. The genera defined here do not include species with abnormal characteristics that might have come from unrelated taxa; rather, each phylad appears to have produced species via allopatric speciation. Two naturally occurring hybrids, ×*Pachgerocereus orcuttii* (Moran, 1962a), from *Pachycereus pringlei* and *Bergerocactus emoryi* and ×*Myrtgerocactus lindsayi* (Moran, 1962c, 1963) from *Myrtillocactus cochal* and *B. emoryi* are evolutionary deadends with very limited distributions, and *Lemaireocereus thurberi* var. *littoralis*, whether or not it is a hybrid, is also very restricted. Less than one-third of the Mexican columnar cacti have been cytologically examined, but from data already collected, polyploidy appears to be uncommon in these species. Therefore, one may assume that changes in base number and in level of ploidy have not been important in the evolution of these columnar species.

Although cacti in general are noted for their ability to root from stem cuttings, most Pachycereeae reproduce in nature only from seeds. No studies have determined whether seeds of these species are ever apomictic.

Several authors (Axelrod, 1960, 1970; Turner, 1972) have suggested that cacti in general and Mexican columnar cacti in particular have old, if not pre-Tertiary, origins. We feel that the family is probably no older than the Miocene, and certainly did not radiate significantly before the Miocene. Evidence for this conclusion must be indirect because verifiable fossils for this family are no older than the Late Pleistocene (ca. 30,000 yr; Van Devender, 1973), when many extant species are recognizable. When the family as a whole is analyzed, about 30% of the extant species, including five species of Pereskioideae, are autochthonous endemics of the Andean Cordillera, which arose only in the Miocene (Solbrig, 1976). Other recent habitats with endemic species are the islands off the coast of Mexico, the Galapagos Islands, and certain islands in the

West Indies. In addition, many of the North American species of Opuntioideae are obviously recent in origin, and *Mammillaria*, the largest cactus genus, with about 20% of the total species, has speciated predominantly in Mexico after very local geographical isolation. Very recent geographical isolation of populations has caused taxonomic problems for genera in North and South America for which no one can agree on the gaps between species. Bird dispersal of seeds from juicy fruits also has promoted geographical isolation of populations in this family. Moreover, once a cactus population is established, plants are likely to survive long periods because they are succulents or, in a few cases, they have the ability to reproduce apomictically. Cactus flowers are attractive to numerous pollinators because they have copious pollen and nectar; therefore, obtaining a new pollinator after arriving in a new area is probably not a major problem. In addition, a number of species appear to be self-compatible. Consequently, many aspects of these organisms are favorable for speciation.

Opinions that Mexican columnar cacti are bradytelic relicts certainly were based on and biased through analyses of the northernmost species, the ultimate derivatives of phylads derived from tropical southern Mexico. When the phylogeny is reconstructed using all available features, morphological gaps between species are small indeed; in fact, character evolution has been very gradual from one species to another. To account for the total number of Mexican Pachycereeae from an initial population, one can propose successful dichotomies on the average of every three million years. This amount of time for speciation is not only realistic but also, in some cases, overgenerous. Speciation in northern Mexico has been encouraged by geographical isolation from the south, e.g., *Carnegiea* and *Lophocereus*; during periods of climatic change, e.g., *Stenocereus alamosensis* and S. *thurberi*; or by habitat isolation within the Sonoran Desert, e.g., *L. gatesii* in southern Baja California. Analyses of paleofloras in Mexico may help us to make intelligent guesses on the age of habitats in which extant species occur and may suggest a time of radiation.

If the phylogeny presented here is relatively correct, flowers have converged a number of times to bat, hummingbird, and hawkmoth pollination since the radiation of the tribe in Mexico. The families of these animals that act as pollinating agents are mostly Tertiary in age, and, in some cases, probably post-Miocene, e.g., the phyllostomatid bats (Koopman & Jones, 1970). Because these cacti have radiated to utilize these large pollinators, it is not likely that the cactus radiation occurred before the pollinators were present. Other organisms that use cacti are species of *Drosophila*, which feed within the rots of columnar cacti and platyopuntias (Fellows & Heed, 1972; Richardson et al., 1977). Throckmorton (1975) suggested that the lineage giving rise to the cactophilic *repleta* and *nannoptera* groups arrived perhaps by mid-Oligocene and radiated later during Oligocene and Miocene times in mountains and developing deserts. Because species of *Drosophila* often feed on only one or a limited number of cactus species, it is reasonable to assume that the timing of the evolution of columnar cacti and their *Drosophila* was relatively synchronous.

Because few species of the West Indies and northern South America have been studied here, no conclusions on the phylogenetic relationships of tribe

Pachycereeae to other columnar forms is justifiable. Nevertheless, similarities observed in available materials suggest that Pachycereeae are most closely related to Browningeae and *Armatocereus* and *Samaipaticereus* (Leptocereeae), all of northwestern South America. *Armatocereus* is very close to Pachycereeae, but Mexican Pachycereeae are likely not closely related to the very specialized species of *Armatocereus* of Central America. We have no way to determine whether progenitors of Pachycereeae migrated through Central America to Mexico or seeds were long-distance dispersed from northern South America. Moreover, data are lacking to determine whether Mexican species of *Cephalocereus* have evolved directly from other Mexican Pachycereinae or originated in northern South America.

Addendum: Additional Collections

In June, 1978, the senior author collected in Nueva Galicia, Mexico, seven more columnar cacti, including one genus and four species not sampled in the initial study plus three more collections of stenocerei. The additional species provide a test for predictions embodied in the proposed phylogeny.

Backebergia militaris (*Gibson 3433*, ARIZ). Stems eventually blackening when cut; skin hard, extremely brittle; epidermis uniseriate, covered by thick (18 μm), rough cuticle; stomates not sunken; hypodermis thick (380–450 μm); silica bodies and crystals absent in skin; outer cortex in ribs composed of radially elongate chlorenchyma, as in *Pachycereus*; mucilage cells abundant in ribs, cortex of axis, and pith; phloem fibers very late in development; starch storage mainly in pith.

Pachycereus grandis (*Gibson 3440*, ARIZ). Stems blackening immediately when cut; skin hard, brittle; epidermis biseriate, covered by very thick (35 μm), rough cuticle; stomates slightly sunken; hypodermis thick (400–460 μm); silica bodies and crystals absent in skin; outer cortex in ribs composed of markedly elongate chlorenchyma developing secondary walls in age; mucilage cells essentially absent; phloem fibers late in development; starch storage not abundant.

Neobuxbaumia mezcalaensis (*Gibson 3412*, ARIZ). Stems remaining green when cut; skin hard, brittle; epidermis uniseriate, covered by cuticle 3.5 μm thick and thick epicuticular wax; stomates not sunken; hypodermis moderately thick (150–210 μm); several small prismatic crystals of calcium oxalate in epidermis and solitary large ones in hypodermis, as in *Cephalocereus*; mucilage cells absent; phloem fibers apparently absent; starch storage abundant in cortex of axis and pith, starch grains largest in pith.

Stenocereus quevedonis (*Gibson 3441*). Stems turning orange when cut; epidermis mostly biseriate, covered by relatively thin (3 μm), smooth cuticle; stomates not sunken; hypodermis moderately thick (210–250 μm); silica bodies in epidermis (3–6 μm) and hypodermis (12–18 μm), resembling those of *S. thurberi*; mucilage cells large, not close to hypodermis, large and abundant throughout stem; starch storage dispersed throughout ground tissue.

Stenocereus kerberi (*Gibson* 3359, ARIZ); *Stenocereus* aff. *montanus* (*Gibson* 3381, ARIZ); and *S. pruinosus* (*Gibson 3429*, ARIZ). Features as described in text; silica bodies present in skin.

Backebergia militaris certainly belongs next to *Pachycereus*. The skin of *Backebergia* resembles those of arborescent *Pachycereus*, and the outer cortex has the distinctive elongate chlorenchymatous cells. However, unlike *Pachycereus*, *B. militaris* is highly mucilaginous. A relationship of *Backebergia* to *Lophocereus* is also undeniable. Not only do young stems of *Backebergia* have a similar external appearance and color in fresh-cut tissue but also the smell of fresh and rotting cortex is strongly reminiscent of *Lophocereus*. The eventual blackening of the stem of *B. militaris* is indicative of its inclusion in Pachycereinae. Presently, the chemistry of *B. militaris* is being studied by H. Kircher (sterols and fatty acids) and J. McLaughlin (alkaloids; many present).

These observations give further confidence to the previous treatment and discussion of other genera. No exceptions have been found where silica bodies are absent in any species of *Stenocereus*. Crystal patterns in *N. mezcalaensis* confirm its close relationships to *Mitrocereus* and *Cephalocereus*, and *Pachycereus grandis* has anatomical features common with *P. pecten-aboriginum* and *P. pringlei*.

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THE CLASSIFICATION WITHIN THE JUGLANDACEAE[1]

WAYNE E. MANNING[2]

ABSTRACT

A full description is presented of the Juglandaceae and of the two subfamilies (Platycaryoideae, Juglandoideae), three tribes of the Juglandoideae (Juglandeae, Engelhardieae, Hicorieae), seven genera, with their subgenera and sections. Figures and tables are given to illustrate the evolution of the genera, the comparative classifications within the family, and the comparative interpretations of the parts of the floral envelopes. Diagrams are presented of the position of the carpels, the orientation and type of the stigmas, and the parts of the floral envelopes. A list is given of the 59 species, with the subspecies and varieties of each, including their distribution.

This article on the Juglandaceae of the world brings together full descriptions of morphological features of the family, subfamilies, tribes, genera, subgenera, and sections, as well as a list of species. Published descriptions are scattered through the literature. Many of the family and generic descriptions are found in regional taxonomic treatments, primarily for members native to the United States, and hence are incomplete, such as Sargent (1933), Rehder (1940), Fernald (1950), and Gleason (1952); few descriptions are given of lesser categories between the ranks of family and genera and genera and species. Modern descriptions of the family applicable to world-wide members are available in works such as Koidzumi (1937), Manning (1952, 1970, 1974), Melchior (1964), Hutchinson (1959, 1967), Elias (1972), and a few others. Engler (1889), Koidzumi (1937), and Melchior (1964) give descriptions of genera, but only Hutchinson (1967) presents rather full descriptions of all (8) modern genera. Some descriptions contain scattered inaccuracies; most do not include all of the variations which occur in the taxa.

This paper describes some features not normally included, such as the nature of early scales and buds and leaves on the seedlings. New information comes from the reassessment of the cross sections of the bases of *Engelhardia* fruits, and of the timing of the appearance of the staminate catkin buds in *Pterocarya rhoifolia*.

A new classification within the family is necessary in order to show the true relationships of genera. The most complete classifications to date are given in Oersted (1870a, 1870b), Koidzumi (1937), Leroy (1955), and Melchior (1964), the taxa of the last two being invalidly published. Elias (1972) also discusses the classifications, but does not propose any formal treatment. In these publications the arrangement of genera is based primarily on fruits, their sizes, and structure of organs involved in dissemination, such as wings or husk. Stone (1973) has suggested that the obvious fruit characteristics are in large part ecological, not necessarily indicative of relationships.

Studies in type and position of inflorescences, nature of parts of floral

[1] I wish to thank Dr. Donald E. Stone for his careful checking of the manuscript, and Dr. Carroll E. Wood, Jr. for his help with problems in nomenclature.

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ANN. MISSOURI BOT. GARD. 65: 1058–1087. 1978.

0026-6493/78/1058–1087/$03.05/0

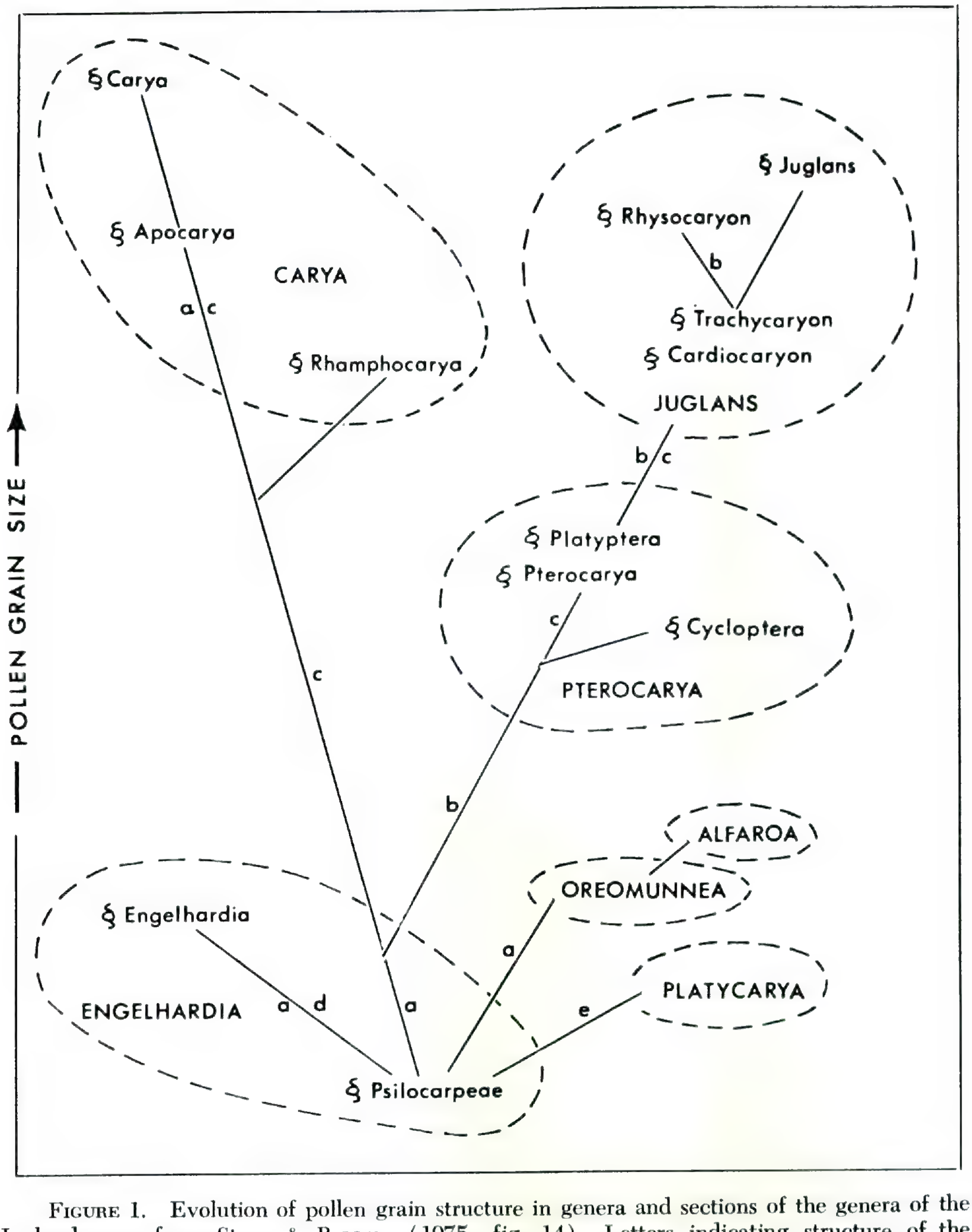


FIGURE 1. Evolution of pollen grain structure in genera and sections of the genera of the Juglandaceae, from Stone & Broome (1975: fig. 14). Letters indicating structure of the pollen grains are explained in that article. Course of evolution shown is very close to my opinion of relationships, except that *Platycarya* is more advanced judging from wood anatomy and floral structure.

envelope, wood anatomy, seedling anatomy, and pollen types of members of the family (Manning, 1938, 1940, 1948; Kribs, 1927; Heimsch & Wetmore, 1939; Whitehead, 1963, 1965; Conde & Stone, 1970; Stone, 1970; Stone & Broome, 1975) agree in general as to the relationships and relative primitiveness and

advancement of genera and even species, and the results are quite different from those of most published classifications.

I have given an outline of my suggested classification in *Encyclopedia Britannica* (Manning, 1974), but only two of the taxa below the family level have descriptions. The present paper is an amplification of that classification, with necessary descriptions, cross references, and a Latin diagnosis where necessary. Since I wrote the 1974 article I have decided not to recognize *Cyclocarya* as a genus (Manning, 1975); hence there are now seven genera. The key to genera and the descriptions of the subfamilies and tribes identify the characters of most diagnostic value. In addition, discussions of relationships of the genera are presented under *Platycarya*, *Pterocarya*, *Engelhardia*, and *Carya* as bases for the classification. Figure 1, based on fig. 14 of Stone & Broome (1975), shows how clearly the evolution of pollen grain structure parallels my opinion of the relationships of the genera and even the sections of the genera as shown in my classification. Table 1 shows the differences between the present classification and those of previous writers, especially for the location of genera.

The only complete list of species of the family is given in Manning (1948). There have been many changes in the last 30 years, and it is necessary to update the list. It seems unnecessary to give citations for the species, subspecies and varieties. The principal publications involved in the changes of names are Iljinskaya (1953), Jacobs (1960), Manning (1949, 1950, 1951, 1957, 1959, 1960, 1966, 1975), Stone (1968, 1972, 1977). Dr. Stone and I now recognize seven genera and 59 species. The species, subspecies and varieties which I recognize, and their distribution, are listed in Table 3 (p. 1083) arranged according to the classification used in this paper. Sargent (1933) and Steyermark (1963) recognize other varieties (and forms), especially for *Carya*.

Terminology and Interpretation

There has been considerable variation among authors in terminology applied to the unit within the catkin. In this paper I am following my previous terminology (Manning, 1938, 1940, 1948); that is, the unit includes the pedicel (unless absent), floral receptacle, subtending bract, two bracteoles (unless absent), 4 or fewer sepals, stamens (in staminate flower), pistil (in pistillate flower). Of the total of 7 (or 9?) leafy organs (the floral envelope) in the most well-developed units, the flower proper consists, of course, of only the sepals (when present) with the stamens or the pistil. However, the subtending bract and barcteoles are united so intimately with the floral receptacle that these seem to be a part of the flower. Consequently, in some cases the description may include the involucre as part of the apparent flower.

A discussion of the terminology with illustrations is given in Manning (1938, 1940, 1948), Hjelmqvist (1948), Abbe (1974) and elsewhere. Abbe, however, has adopted a different terminology for all members of the Amentiferae and a comparison is in order here. In the following statement my terms are given first and Abbe's equivalent follows in parentheses. Floral unit of the catkin, the apparent flower, with its involucre, calyx or stamens or pistil (partial staminate or pistillate inflorescence); bract (bract or primary bract); bracteoles

TABLE 1. Comparative list of classifications within the Juglandaceae, subfamilies, tribes, genera; arranged to show comparisons, not in the order of the authors; numbers and letters show the latter.

OERSTED 1870 (not called tribes)	KOIDZUMI 1937	LEROY 1955 (no Latin descr., no types)	MELCHIOR 1964 (no Latin descr., no types)	MANNING 1978
C. PLATYCARYEAE	I. NUCIFEROIDEAE	II. OREOMUNNOIDEAE	I. PTEROCARYOIDEAE	I. PLATYCARYOIDEAE
	A. PETROPHILOIDIEAE		A. PLATYCARYEAE	
6. *Platycarya*	1. *Petrophiloides*	8. *Platycarya*	1. *Platycarya*	1. *Platycarya*
				II. JUGLANDOIDEAE
A. ENGELHARDTIEAE	B. PTEROCARYEAE		B. PTEROCARYEAE	B. ENGELHARDIEAE
1. *Pterocarya*	2. *Pterocarya*	4. *Pterocarya*	2. *Pterocarya*	
2. *Engelhardtia*	3. *Engelhardtia*	7. *Englehardtia*	3. *Engelhardia*	4. *Engelhardia*
3. *Oreomunnea*		6. *Oreomunnea*	4. *Oreomunnea*	5. *Oreomunnea*
		5. *Alfaroa*		6. *Alfaroa*
	II. DRUPOIDEAE	I. JUGLANDOIDEAE	II. JUGLANDOIDEAE	
B. JUGLANDEAE VERAE	C. ALFAROEAE		A. ALFAROEAE	
	4. *Alfaroa*		5. *Alfaroa*	
	B. CARYEAE		B. JUGLANDEAE	A. JUGLANDEAE
4. *Juglans*	5. *Juglans*	1. *Juglans*	6. *Juglans*	2. *Juglans*
				3. *Pterocarya*
				C. HICORIEAE
5. *Carya*	6. *Carya*	2. *Carya*	7. *Carya*	7. *Carya* (incl. *Annamocarya*)
		3. *Annamocarya*	8. *Annamocarya*	

TABLE 2. Comparison of interpretation of floral enveolpe by different authors. Key to abbreviations at bottom of table.

	MANNING	EICHLER	NAGEL	HJELMQVIST	HUTCHINSON
Platycarya:	♂: B * *	B * *	B * *	B * *	B * *
			[Bbb] *	[Bbb] *	
	♀: B [b 1] [b 1] (3, 4)	B bb *	B * 4	[Bbb] 4	B * 2,3
Juglans:	♂: B bb (14)4–1	B bb 4–2	B * 6–4	B bb 4–1	B * 6,5
			B bb 6–4		
	♀: B bb 4	B bb 4	B bb 4	B bb 4	B bb 4
				B bbb′ 4	
Pterocarya:	♂: B bb 4–1	B bb 4–2	B * 6–4	B * 4	B * 6–3
				B bb 4–1	
	♀: B bb 4	B bb 4	B bb 4	B bb 4	B bb 4
Engelhardia:	♂: B3 bb 4–1(0)	[Bbb] 4	[Bbb] 4–3	[Bbb] 6–4	B * 6–3
	B3 * 4–0			[Bbb] 4,3,0	
	♀: B3 bb 4	[Bbb] b′b′ 4	[Bbb] b′b′ 4	[Bbb] b′b′ 4	B3–5 * 4
		[Bbb] 4			
Oreomunnea:	♂: B3 bb 4–2	– – – –	– – – –	[Bbb] 6–3	B * 5–3
	♀: B3 bb 4	– – – –	– – – –	[Bbb] b′b′ 4	B3–5 * 4
Alfaroa:	♂: B3 bb 4–2	– – – –	– – – –	[Bbb] 5	B * 5,4
	♀: B3 bb 4	– – – –	– – – –	[Bbb] 4	B3 * 4,5
Carya:	♂: B bb *(1, 2)	B bb *	B bb *	B * 2,3	B * 2,3
	♀: B bb (st.d.)	B bb 1	B bb 1	Bbbb′ (4?)	(B) * 4
	B bbb′b′b′? *				

B, bract; b, bracteole; b′, extra bracteole; B3,B3–5, 3- or 3- to 5-lobed bract; [Bbb], bract and bracteoles fused to form a 3-lobed structure; [b 1], bracteole and a sepal fused to form a lateral appendage; st. d., stigmatic disc, modified calyx?; numbers in last column of each author, numbers of sepals; *, organs absent.

(secondary bracts); extra bracteoles (tertiary bracts); flower (floret); receptacle (torus); calyx or perianth (perigon); sepals (tepals).

There is wide diversity of opinion among authors concerning the nature or interpretation of the parts of the floral envelope, that is, of the bract, unlobed or lobed, bracteoles and sepals. Manning (1940, 1948), Iljinskaya (1953), and Abbe (1974) have summarized the interpretations of various authors, especially of Eichler (1878), Nagel (1914), Hjelmqvist (1948), Leroy (1955), and Hutchinson (1967). Interpretations that differ from mine are given in parentheses: (1). STAMINATE FLOWERS. *Pterocarya* and *Juglans*: bract, 2 bracteoles, 4 or fewer sepals (bract, no bracteoles, 6 or fewer sepals); *Engelhardia, Oreomunnea, Alfaroa*: 3-lobed bract, 2 bracteoles beside the 4 or fewer sepals (bract and 2 bracteoles fused into a 3-lobed structure, no bracteoles beside the 6 or fewer sepals); *Carya*: bract, 2 bracteoles, with rarely 1 or 2 sepals (bract, no bracteoles, 2 sepals with rarely one or 2 other sepals); *Platycarya*: bract (bract, or bract and 2 bracteoles as a slightly 3-lobed structure). (2) PISTILLATE FLOWERS. *Pterocarya*: bract, 2 bracteoles separate or united, 4 sepals (bract, 2 bracetoles, 4 sepals); *Juglans*: as in *Pterocarya*, but the apices of the bracteoles often split into 3 or 4 segments (bract, 2, 3, or 4 bracteoles, 4 sepals); *Engelhardia, Oreomunnea, Alfaroa*: 3-lobed anterior bract, 2 posterior bracteoles, these often reduced, 4 sepals (bract and 2 bracteoles fused into one 3-lobed structure, 1 or 2 additional posterior bracteoles often present, 4 sepals; *Carya*: bract, 2 bracteoles whose tips are divided into 3–5 structures, or possibly bract and 3–5 bracteoles, stigmatic disc (where present) probably a modified calyx (bract, 2 bracteoles, 1 sepal, or bract, 3–4 bracteoles, 1 sepal, or low bract, 4–6 sepals, or bract, 2–4 bracteoles, and an inner circle of 2–4 "sepals"); *Platycarya*: bract, 2 lateral appendages each consisting of the fusion of a bracteole and a sepal, and sometimes 1 or 2 anterior-posterior sepals (bract, 2, 3, or 4 sepals, or bract, 2 bracteoles, no sepals, or bract and 2 bracteoles fused into a somewhat 3-lobed structure, 2–4 sepals).

The different interpretations of the floral envelopes depend primarily on whether the 2 lateral organs inside the bract in the staminate flowers are bracteoles or sepals; whether the 3-lobed anterior structure in staminate and pistillate flowers of *Engelhardia, Oreomunnea,* and *Alfaroa* represents a 3-lobed bract or the fusion of a bract and 2 bracteoles; whether the organs in the pistillate flower of *Carya* are, in part or entirely, sepals instead of the bract and bracteoles; whether the lateral appendages in *Platycarya* consist of the fusion of bracteoles and sepals, or are bracteoles alone, or sepals alone.

Table 2 compares my interpretation of the floral envelope with that of four other authors. The terminology used in this paper is based on a comprehensive study of all known species in the family, with special emphasis on the inflorescences, pistillate and staminate flowers, and fruits (Manning, 1926, 1938, 1940, 1948). Leroy (1955) has studied the floral anatomy of the pistillate flowers and fruit and Berquam (1975) that of the staminate flowers.

In the pistillate flowers of *Engelhardia* and its relatives, Leroy (1955) has interpreted the anterior (abaxial) structure as a bract and 2 bracteoles. However, Crepet et al. (1975) and Dilcher et al. (1976) have shown that the 3-lobed bracts

of fruits and staminate flowers of fossil relatives of *Engelhardia* in the Eocene are very similar to those of modern members; the ancestral condition of the fruiting bracts seems to have been a broad slightly 3-lobed bract (see also Manning, 1940: fig. 25) somewhat similar to the occasional, slightly 3-lobed bract in *Platycarya*. Berquam (1975) interprets the 3-lobed structure as a 3-lobed bract, thus supporting my interpretation for *Engelhardia*, *Oreomunnea*, and *Alfaroa*.

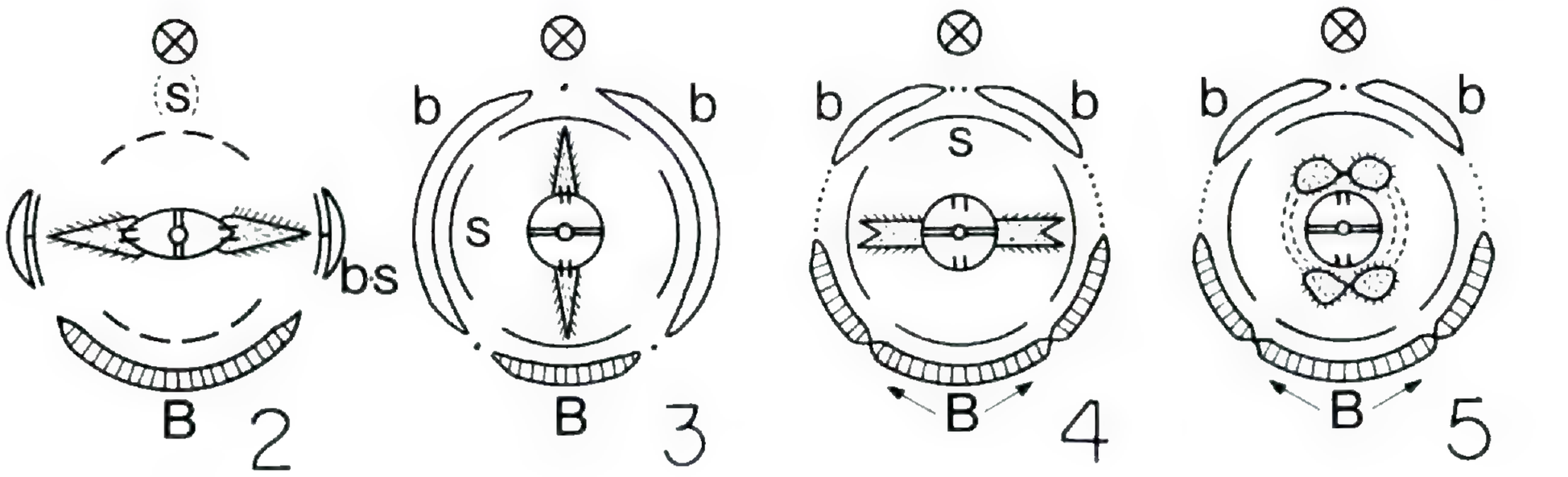
The interpretation above indicates in turn that the most fully developed staminate flowers of most genera (not including the greatly reduced flowers in *Carya* and *Platycarya*) normally have 6 organs besides the bract. Thus the number is identical to that in the pistillate flowers, where the interpretation of 2 bracteoles and 4 sepals is rather definite. Berquam (1975), on the other hand, did not find any anatomical differences between what I have called the bracteoles and the sepals, and thus interprets the 6 organs as 6 "tepals." Abbe (1974) has pointed out that the study of the development of the staminate flowers by Macdonald (1971) indicates that the outer organs (bracteoles) differ from the 4 inner ones.

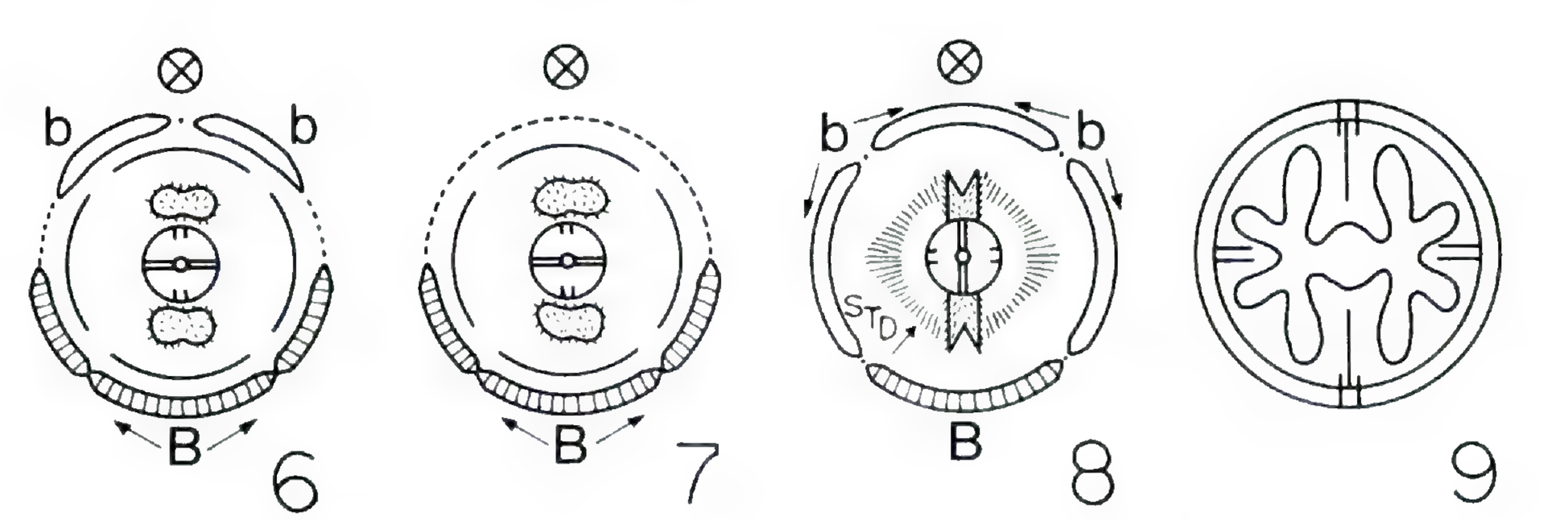
The 4 foliar organs in the pistillate flowers of *Carya* sections *Carya* and *Apocarya* are clearly involucral, not calyx or in part calyx, because of their structure, arrangement, and vascular anatomy. Furthermore, Hjelmqvist (1948) has found 1–4 "sepals" inside of this involucre in a few flowers of a few species, and I have interpreted the stigmatic disc as a modified calyx. Whether the 3 structures besides the bract represent 2 bracteoles whose tips are split into 3 structures or 3 bracteoles is uncertain. In section *Rhamphocarya*, where there are 5 structures besides the bract, Leroy (1955) (using the generic name *Annamocarya*) believes that some of these are bracteoles and others (which ones uncertain) are sepals. A stigmatic disc seems absent in this section.

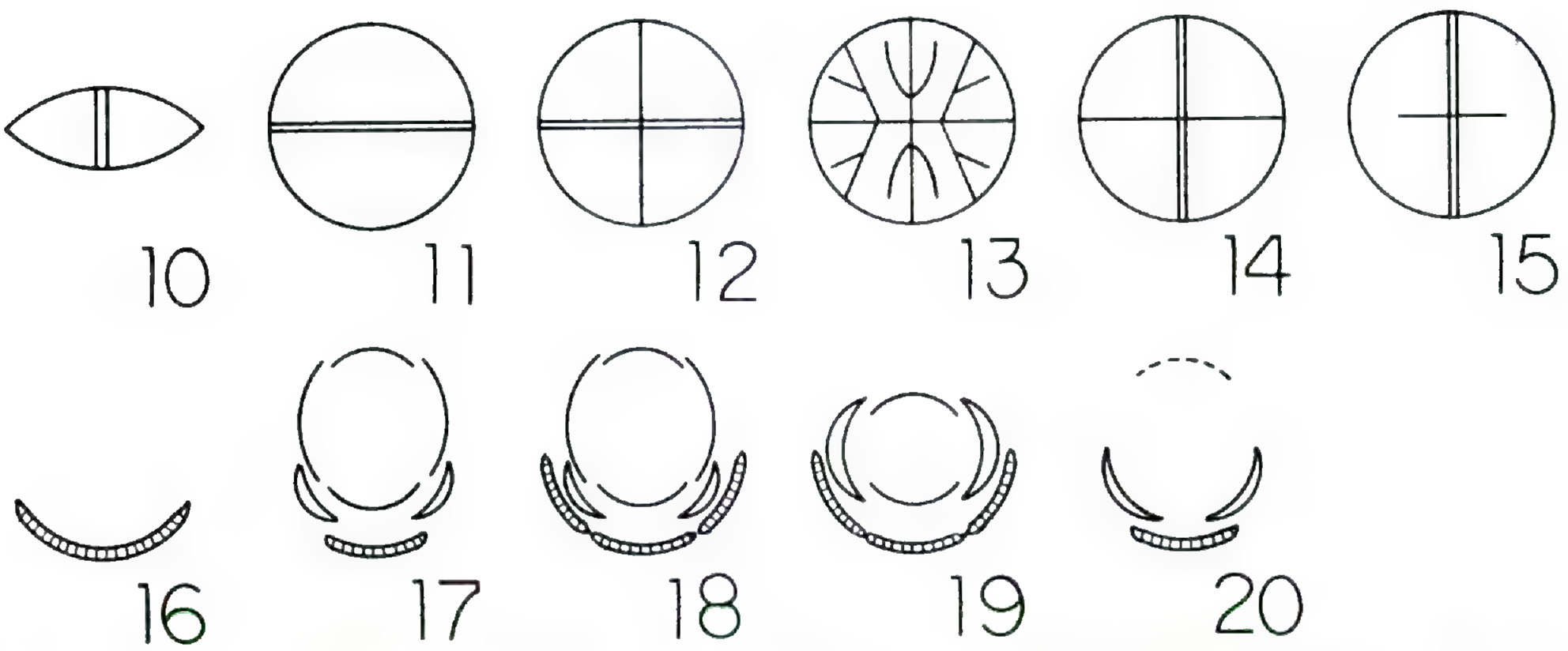
In the broad bract of the pistillate flowers of *Platycarya* the floral anatomy is more complex than in the narrow bract of most genera; the structure is occasionally 3-lobed, suggesting to some authors a bract and 2 bracteoles. However, the organ is probably a primitive one, and the 3-lobed structure probably represents a structure similar to that in the fossil relatives of *Engelhardia* mentioned previously. Furthermore, if the bracteoles are not present in the bract complex, each of the 2 lateral appendages, with a slightly double aspect, could represent a bracteole, in part. In addition, there is a vascular supply to the organ from the base of the flower, shown in Manning (1926) and in Leroy (1955), and also a separate vascular supply to the organ high in the flower.

→

FIGURES 2–20. Diagrams of flower and fruit structure of genera and generic sections of the Juglandaceae. Orientation with reference to the bract and axis of the catkin is the same in all figures, except Fig. 9.—2–8. Diagrams of the typical structure of the pistillate flowers in all 7 genera, showing the orientation of the 2 carpels with reference to the bract and axis of the catkin (only primary partition shown), orientation and shapes of stigmas, location of lines of dehiscence of the fruits (short double line at right angles to the primary partition), and the parts of the floral envelope present.—2. *Platycarya*.—3. *Juglans*, *Pterocarya*.—4. *Engelhardia*, sect. *Engelhardia*.—5. *Engelhardia*, sect. *Psilocarpeae*.—6. *Oreomunnea*.—7. *Alfaroa*.—8. *Carya*.—9. Diagram indicating, for all genera, the location in the







fruits of the two 4-lobed cotyledons of the embryo, one cotyledon in each valve (right and left), not carpel, of the fruit; folding and enlargement of cotyledons not shown, as diagram is essentially the condition of the embryo in the upper part of the loculus of a young ovary; primary and secondary incomplete partitions and lines of dehiscence indicated, though secondary partition absent in some genera; orientation of carpels with reference to axis depends upon the genus.—10–15. Diagrams of cross sections of nuts and nutlets in all genera showing typical presence of primary (double line) and secondary (single line) incomplete partitions at base of fruit, thus indicating number of "cells" at base of fruit; lines of dehiscence, secondary and tertiary internal projections, and lacunae are not indicated, except in Fig. 13.—10. *Platycarya*.—11. *Juglans*, sections *Cardiocaryon* and *Trachycaryon*; *Pterocarya*, subgen. *Cyclocarya*.—12. *Juglans*, sections *Dioscaryon* and *Rhysocaryon*; *Pterocarya*, sections *Pterocarya* and *Platyptera*; *Engelhardia*.—13. *Oreomunnea*, *Alfaroa*; tertiary incomplete septa, with internal projections, shown at one level.—14. *Carya*, sections *Carya* and *Apocarya*; *Pterocarya*, sect. *Pterocarya*, occasional variation.—15. *Carya*, sect. *Rhamphocarya*.—16–20. Floral diagrams for the staminate flowers, showing the parts of the floral envelope present in the most fully developed flowers; variation in parts not shown; that is given in Manning (1948).—16. *Platycarya*.—17. *Juglans*, *Pterocarya*.—18. *Engelhardia*, sect. *Engelhardia*; *Oreomunnea*; *Alfaroa*.—19. *Engelhardia*, sect. *Psilocaryeae*.—20. *Carya*. B, bract, unlobed and 3-lobed, structure cross lined; b, bracteole, structure not lined; b-s, lateral appendage, bracteole and sepal fused; s, sepal, single line; st d, stigmatic disc, probably modified calyx.

This combination is similar to that of the bracteoles and sepals in *Pterocarya* and *Juglans*, so I believe that the interpretation of the lateral appendage as a fusion of a bracteole and a sepal is correct, even though there are occasional flowers with 1 or 2 additional organs, making 3 or 4 organs apparently in a ring, resembling 4 sepals.

Figures 2–8 show diagrammatically the typical structure of the pistillate flowers in all 7 genera, the orientation of the carpels with reference to the bract and the axis of the catkin (only primary partition shown), the orientation and shapes of the stigmas, the location of the lines of dehiscence of the fruit (at right angles to the primary partition), and the parts of the floral envelope present. Figures 10–15 show diagrammatically in all genera the typical presence of the primary and secondary incomplete partitions at the base of the fruit; the lines of dehiscence, the secondary and tertiary internal projections, and the lacunae are not indicated, except in Fig. 13. Figures 16–20 illustrate for the staminate flowers the parts of the floral envelope present in the most fully developed flowers; the variation in parts present is not shown; this aspect is described and illustrated in Manning (1948). Figure 9 diagrammatically shows the location of the two 4-lobed cotyledons in the fruits, one cotyledon in each valve (not carpel) of the fruit.

JUGLANDACEAE A. Rich. ex Kunth, Ann. Sci. Nat. (Paris) 2: 343. 1824, "Juglandeae," nom. cons.

Trees or rarely large shrubs, mostly with abundant tannin; buds naked or scaly; terminal buds present, the lateral often several superposed; leaf scars large, with 3 groups of vascular bundle scars; pith solid or chambered; leaves deciduous or rarely evergreen, alternate, rarely opposite or whorled, exstipulate, pinnately compound, often aromatic; leaflets (3–)5–31, entire or serrate; leaves, buds, flowers, fruits commonly resin dotted (glandular dotted, lepidote) with yellow or pale several-celled peltate glandular scales in various amounts; hairs often fascicled or glandular; flowers unisexual, wind pollinated, typically dichogamous; plants monoecious or rarely dioecious, staminate or pistillate flowers or both in elongate drooping or rarely erect catkins or spikes; staminate and pistillate inflorescences sometimes separate, sometimes combined into an androgynous panicle with the central spike wholly or partly pistillate and the lateral branches staminate; separate staminate inflorescence a cluster of 3–8 catkins or a solitary catkin; separate pistillate inflorescence a many-flowered catkin or a 2- to several-flowered spike; inflorescences terminal, or lateral on old wood, or the staminate sometimes at the base of new growth; flowers 1 to a bract, apetalous; sepals in staminate flowers 4, or reduced in number or lacking, often irregular, the entire or 3-lobed bract and 2 bracteoles (when present) fused with the floral receptacle and appearing as part of the calyx, stamens thus appearing to be on the involucre and calyx; stamens 3–105, sessile, the anthers longitudinally dehiscent; rudimentary pistil rarely present; pistillate calyx usually 4-lobed, fused with the ovary, or absent, the subtending bract and 2 (or 3 or 4?) bracteoles fused only with the pedicel and base of the ovary or with the whole ovary, a ring of minute inner bractoles very rarely present; a few stamens present in individual flowers

of a few species of certain genera; pistil bicarpellate, or very rarely in individual flowers with 3 or 4 carpels; ovary inferior, 1-locular, with 1 true incomplete partition and often with a false secondary one or even a tertiary one, thus 2- or falsely 4- to 8-celled below, 1-celled above the middle, sometimes falsely 5-celled at the very apex due to intrusions from the wall, thus matching the 4-celled condition at the base of the ovary; lower part of the loculus in the immature ovary usually filled with packing tissue; ovule 1, erect, orthotropous, with a single integument, located at the top of the primary partial partition; placentation modified axile, but at first superficially appearing basal; style 1, rarely absent, with 2–4 stigmatic branches; fruit a nut enclosed in an adherent thin or thick fibrous indehiscent or dehiscent husk, or a nut with a thin dry skin, or a thin-skinned nutlet with 2 or 3 wings or 1 circular one; whole fruit drupelike, but the husk derived from the involucre and the calyx, and the skin from the calyx alone, neither one from the pericarp, hence fruit not a true drupe, sometimes called a tryma; nut or nutlet loculicidal in germination; seed solitary, large, 2- to 4- to 8-lobed, without endosperm, filling the cavity of the nut or nutlet; cotyledons 4-lobed, often fleshy, oily, at germination remaining in the nut or nutlet or appearing above ground as 4-lobed leaves; chromosome number $n = 16$ or rarely $n = 32$; fertilization chalazogamous.

TYPE: *Juglans* L.

Seven genera, 59 species; distribution North, Central and South America, West Indies, eastern Asia, Japan, Philippines to East Indies, Himalayas, southwestern Asia, and southeastern Europe (Caucasus Mountains).

Key to Genera of the Juglandaceae

a. Bracteoles and sepals absent in staminate flowers; inflorescences (panicles of catkins) terminal at the tip of main shoots and also at the tips of short axillary shoots just below those panicles; staminate and pistillate catkins many-flowered, erect; pistillate and fruiting inflorescences condensed, conelike; pistillate catkins usually tipped by a staminate one; carpels transverse; fruits very small, narrowly 2-winged; leaves odd-pinnate; leaflets serrate; pith solid; buds scaly ..... 1. *Platycarya*

aa. Bracteoles and usually 1 or more sepals present in staminate flowers; inflorescences (panicles of catkins or solitary catkin or spike) terminal on the main shoots or lateral on old wood at the base of new growth; staminate catkins drooping; pistillate inflorescences either few-flowered and erect or if many-flowered then slender, elongate, drooping; pistillate catkins completely pistillate; carpels median or transverse; fruits small to large, either not winged or broadly winged; leaves odd- or even-pinnate; leaflets serrate or entire; pith solid or chambered; buds scaly or naked.

b. Definite sepals absent in pistillate flowers (only the single row of involucral organs present; carpels transverse; stigmas commissural, hence anterior-posterior; bracts not 3-lobed; staminate catkins in clusters of 3–8 at the base of new growth; leaves odd-pinnate; pith solid; fruits rather large nuts with a husk slightly to strongly dehiscent along the 4–6 ridges; buds scaly ..... 7. *Carya*

bb. Definite sepals present in pistillate flowers (a row of 4 organs inside that of the involucre); carpels median (anterior-posterior); stigmas carinal or commissural; bracts sometimes 3-lobed; staminate catkins solitary of if clustered, terminal on new growth or lateral on old growth; leaves odd- or even-pinnate; pith solid or chambered; fruits winged or if with a husk this mostly indehiscent; buds scaly or naked.

c. Pistillate and staminate infloresecences in different locations, the pistillate terminal, the staminate lateral; bracts of all flowers narrow, unlobed; fruits

with 2 lateral or 1 circular wing or with a thick husk; leaves alternate, mostly odd-pinnate; pith chambered; staminate catkins mostly solitary (in clusters of 3–5 in one species of *Pterocarya*); buds naked or scaly.

d. Fruits winged nutlets; bract scalelike at the base of the fruit or at the outer margin of a circular wing; staminate inflorescenses stalked solitary catkins or stalked clusters of 3–5; buds naked or scaly; germination epigeal ..... 3. *Pterocarya*

dd. Fruits nuts with a husk; bract fused with the ovary to its apex and involved in the husk; staminate catkins solitary, sessile, though often superposed; buds scaly; germination hypogeal ..... 2. *Juglans*

cc. Pistillate and staminate inflorescences in the same location in a given species, both terminal or both lateral, the two sexes often combined in an androgynous panicle; bracts of flowers 3-lobed, usually comparatively broad; fruits thin- to thick-skinned, either not winged or with an anterior large 3-lobed wing; leaves alternate, opposite or whorled, even-pinnate; pith solid; staminate catkins in clusters of 3–6; buds naked.

e. Leaves alternate; nutlets winged, 2- to 4-celled at the very base; central lobe of wing of fruit with midrib only, not 3-nerved; stigmas (stigmatic style arms) either commissural and elongate or split-carinal, very short, without a style or style arms; trees of the Old World ..... 4. *Engelhardia*

ee. Leaves opposite or whorled; nuts or nutlets 8-celled at the base or middle; stigmas carinal, almost round, at the tips of elongate style arms; trees of the New World.

f. Fruits nuts within a thin to thick skin, the bract a minute scale at the base of the fruit; adaxial bracteoles reduced to a mere rim ..... 6. *Alfaroa*

ff. Fruits winged nutlets with a thin skin, the bract developing into the large anterior 3-lobed wing, the central lobe of the wing trinerved; bracteoles developing into a rather prominent 2-lobed posterior flap enclosing the nutlet ..... 5. *Oreomunnea*

SUBFAM. I. PLATYCARYOIDEAE Mann., stat. nov.

Tribe(?) Platycaryeae Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbhavn 1870a: 172; 1870b: 2. TYPE: *Platycarya* Sieb. & Zucc.

Tribe Platycaryeae Nakai, Fl. Sylv. Koreana 20: 76. 1933. TYPE: *Platycarya* Sieb. & Zucc.

Tribe Petrophiloidieae Koikzumi, Acta Phytotax. Geobot. 6: 10. 1937. TYPE: *Petrophiloides* Bowerbank = *Platycarya* Sieb. & Zucc.

Pith solid; bud scales present; leaves alternate; leaflets serrate; fruiting catkin condensed, conelike, many-fruited, erect, the unmodified, rather broad, unlobed or rarely slightly 3-lobed elongate bracts woody, rigid, prominent, projecting far beyond the nutlets and hiding them; the very small narrowly 2-winged nutlets falling off the tree, separating from the fruiting bracts, the bracts persisting on the tree as cone-scale-like structures; nutlets strongly flattened anteriorly-posteriorly (lateral with regard to carpels) and with 2 narrow lateral wings; fruiting catkin and nutlets resembling those of *Betula*; inflorescences terminal on the main shoot or also on the upper, very short axillary shoots, consisting of a cluster of short-stalked staminate catkins or a central pistillate catkin surrounded by several staminate ones, all of the catkins erect; pistillate catkin many-flowered, usually tipped by a staminate one, thus the catkin androgynous; bracteoles and sepals absent in the staminate flower; the 2 bracteoles in the pistillate flower inconspicuously fused with the lateral sepals, these together called lateral appendages, the latter fused with the ovary to its apex, 1 or 2 additional median (anterior-posterior) sepals occasionally present; wings of the nutlet developed from the lateral appendages; carpels lateral (transverse), the style absent, the

stigmas elongate, carinal; ovary and nutlet 2-celled at the base; germination epigeal.

TYPE: and only genus, *Platycarya* Sieb. and Zucc.

1. **Platycarya** Sieb. & Zucc., Abh. Math.-Phys. Cl. Königl. Bayer Akad. Wiss. 3: 741. 1843.

Petrophiloides Bowerbank, Foss. Fruits London Clay: 43, *tab. 9, 10.* 1840, cf. Art. 58, *International Code of Botanical Nomenclature* where this is used as an example.
Fortunea Lindl., J. Hort. Soc. London 1: 150. 1846. TYPE: *F. chinensis* Lindl. = *P. strobilacea* Sieb. & Zucc.

The only genus of the subfamily; characters of the subfamily.

Deciduous tree or large shrub; terminal bud prominent; buds scaly; pith solid; leaves odd-pinnate, alternate, exstipulate, the 7–15 leaflets serrate, glandular-dotted beneath; staminate and pistillate inflorescences terminal, on the main shoot or also on the upper short lateral shoots, either combined in an androgynous panicle with the pistillate catkin central surrounded by several staminate catkins or a separate cluster of stalked staminate catkins, all catkins erect; pistillate catkin many-flowered, condensed, conelike, usually tipped by a staminate one with a short intermediate zone of abnormal perfect flowers; bracteoles and sepals absent in staminate flowers; stamens 4–15, apparently located on the surface of the unlobed elongated comparatively broad bract, an abortive pistil sometimes present; bract very rarely with 2 small lobes; anthers glabrous; unlobed bract in the pistillate flower large and stiff, becoming neither husk nor wings, essentially separate from the ovary and fruit; bracteoles minute and fused with the 2 lateral sepals, called lateral appendages, reaching to the apex of the ovary, and forming narrow lateral wings for the nutlet; median pair of sepals occasionally present; carpels transverse (lateral); common style absent; stigmas carinal, elongate, hence also transverse, the stigmatic area on the inner surface of the style arms; fruiting catkin erect, conelike, resembling the fruiting catkin of *Betula*; nutlets very small, 2-celled at the base, 4 mm in diameter including the very narrow lateral wings, strongly flattened anteriorly-posteriorly, falling off from the bracts and from the persistent fruiting catkin; germination epigeal, the cotyledons leaflike, 4-lobed; first true leaves of the seedling above the cotyledons simple, then small compound ones; cotyledonary node 1-gap 2-trace.

TYPE: and only species, *P. strobilacea* Siebold & Zuccarini (including *P. longipes* Wu).

Japan, Korea, China, and Viet Nam.

Platycarya and *Pterocarya* do not belong in the same tribe or subfamily; they are similar only in having small winged fruits, but are different in size of bracts, orientation of carpels, type and position of inflorescences; sepals are completely absent in the staminate flowers of the former genus. As indicated by wood anatomy, pollen type, and final separation of fruit and bract, *Platycarya* has evolved along a different line of development from the rest of the family. Although the size of the bract, the type and position of the inflorescences, and the separation of the fruit from the bract are of primitive types, the wood

anatomy, the complete reduction of sepals in the staminate flowers with the fusion of the flower with the axis of the catkin, and the fusion of the bracteoles and sepals in the pistillate flowers indicate a definite advancement and specialization. Stone (1970) has shown, however, that *Platycarya* and *Pterocarya* have retained similar primitive seedling anatomy.

SUBFAM. II. JUGLANDOIDEAE.

Subfam. Drupoideae Koidzumi, Acta Phytotax. Geobot. 6: 10. 1937, nom. inval.

Pith solid or chambered; buds scaly or naked; leaves exstipulate, alternate, opposite or whorled; leaflets serrate or entire; inflorescences terminal or lateral; fruiting catkin or spike not condensed or conelike, either few-fruited and erect, or many-fruited, elongated and drooping, the bracts not rigid and woody nor resembling cone-scales; fruiting bract remaining attached to the nut or nutlet and falling off the tree with it (in *Carya* the husk in some cases remaining on the tree for a short time); bract unlobed or 3-lobed, becoming modified in fruit as part of the husk, or as a wing or part of the wing, or as a minute scalelike structure at the base of the fruit; catkins or spikes many- to few-flowered, solitary or clustered, at least the staminate catkins elongate, drooping; pistillate catkin not tipped by a staminate one, thus the pistillate catkin or spike completely pistillate; bracteoles present in the staminate flowers and mostly evident in the pistillate ones; definite sepals usually present in the staminate and pistillate flowers (except in *Carya* where sepals are rarely present in individual staminate flowers and are modified in pistillate ones); stamens 3–105; bracteoles in pistillate flowers distinct, at least at the tips, from the sepals when the latter are present; carpels median or transverse, the stigmas carinal or commissural, elongate or subglobose; ovary and fruit 2- to 4- to 8-celled below the middle; fruits not flattened or only slightly so, not minute but small to large, 15 mm or more in diameter including wings or husk; germination epigeal or hypogeal.

TYPE: *Juglans* L.

TRIBE A. JUGLANDEAE.

Tribe(?) Juglandeae verae Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbhavn 1870a: 172; 19780b: 2. LECTOTYPE: *Juglans* L.
Tribe Juglandeae Nakai, Fl. Sylv. Koreana 20: 83. 1933. TYPE: *Juglans* L.
Tribe Pterocaryeae Koidzumi, Acta Phytotax. Geobot. 6: 10. 1937. TYPE: *Pterocarya* Nutt.

Pith chambered; buds scaly or naked; leaves alternate; bract unlobed, narrow, remaining small and narrow in fruit; bracteoles broad, enlarging in fruit into wings or husk; bract free or essentially so from the ovary or fused with it to its tip; bracteoles mostly fused with the ovary, at least on the posterior (adaxial) side; staminate and pistillate inflorescences in different locations, the pistillate terminal, the staminate lateral on old wood or at the base of new wood; sepals typically present in both staminate and pistillate flowers, though often reduced in number in staminate ones; carpels median; short common style present; stigmas carinal, elongate, the plumose stigmatic areas on the inner surface of the recurved style arms, hence also median; fruit a nut with a husk or a winged

nutlet; surface of nutlet rather smooth over the ridges, that of the woody nut shell (pericarp) typically rough ridged externally or rugose, very rarely smooth; nut shell typically with several lacunae in the wall, 2- to 4-celled at the base; germination epigeal or hypogeal.

TYPE: *Juglans* L.

2. **Juglans** L., Sp. Pl. 2: 997. 1753; Gen. Pl., ed. 5: 431. 1754.

Hippocarya Dochnahl, Sich. Fuhr. Obstk. 4: 22. 1860. LECTOTYPE: *H. quadrangularis* Dochnahl = *J. regia* L.
Wallia Alefeld, Bonplandia 9: 335. 1861. LECTOTYPE: *J. nigra* L.

Deciduous trees or large shrubs; pith chambered; buds with a few bud scales, the latter often accrescent in spring, the terminal bud prominent; lateral buds sessile, usually superposed; leaves alternate, odd-pinnate, large, aromatic, exstipulate; terminal leaflet rarely reduced in size; leaflets serrate or entire, glandular-dotted beneath; plants monoecious; staminate catkins lateral, solitary, on old wood, in the axils of leaf scars, sessile, drooping, the immature naked catkins first appearing in late summer in the axils of leaves and persisting over winter as small budlike structures; pistillate spike 2- to 25-flowered, terminal on new leafy growth; staminate and pistillate flowers with bract, 2 bracteoles, and 4 sepals, the sepals in the staminate flowers often reduced in number ("sepals" in some Latin American species frequently 6–14); bract small, narrow, unlobed (occasionally in *J. nigra* with "ears" beside the tip of the bract, so bract 3-lobed?); staminate flower consisting of 7–85(–105) stamens apparently on the bract, bracteoles, and sepals as these are fused with the floral receptacle; anthers glabrous but sometimes slightly pubescent in some species; apparent pistillate flower consisting of bract, 2 bracteoles, whose free tips are variously lobed, and 4 sepals, all fused to the apex with the ovary except for short free tips, so ovary inferior (5 sepals reported in a few individual flowers); carpels 2, median (anterior-posterior), rarely 3–4 in individual flowers on individual trees; style with 2 elongate recurved style branches, the stigmatic areas plumose on the inner surfaces of the style arms; stigmas carinal, hence also median; a ring of inner bracteoles very rarely present (in *J. nigra*); fruit large, drupelike, consisting of a rough-ridged or rarely rugose (or even smooth) nut enclosed in an adherent thick fibrous usually indehiscent husk, the husk derived from the involucre and calyx; wood nut shell (pericarp) usually with prominent wall cavities, 2- to 4-celled at the base; cotyledons fleshy, 4-lobed, straight, 1 cotyledon in each valve (not carpel) of the nut, the cotyledons hypogeal in germination; cotyledonary node 2- to 3- to 4-gap, 2- to 3- to 4-trace.

TYPE: *J. regia* L.

Twenty-one species, North and South America, West Indies, and from southeastern Europe to eastern Asia and Japan.

Sect. a. **Juglans.**

Juglans sect. *Dioscaryon* Dode, Bull. Soc. Dendrol. France 2: 72. 1906. LECTOTYPE: *J. regia* L.
Juglans sect. *Cinerea-Regia*, subsect. *Regia* Nagel, Bot. Jahrb. Syst. 50: 483. 1914. TYPE: *J. regia* L.

Husk usually irregularly dehiscent into 4 valves, easily separating from the nut; nut with thin partitions, externally rugose to almost smooth, with 2 winged ridges (sutures), easily splitting; leaflets 5–9(–11), entire on mature trees; staminate flowers sessile, the receptacle elongate, with 10–28(–40) stamens; pistillate spike 2- to 5-flowered; nut 4-celled at the base, falsely 5-celled at the apex; embryo and seedling with 2 rows of scales with buds, superposed above the cotyledons, then with small spirally arranged compound leaves.

TYPE: and only species, *J. regia* L.
Southeastern Europe, Iran to Himalayas, and China.

Sect. b. **Rhysocaryon** Dode, Bull. Soc. Dendrol. France 11: 165. 1909.

Juglans sect. *Nigra* Nagel, Bot. Jahrb. Syst. 50: 484. 1914. LECTOTYPE: *J. nigra* L.

Husk indehiscent, persistently attached to the nut, which is strongly rough-ridged, but the sharp ridges highly indefinite in number and arrangement, in one species almost smooth, but no winged sutures present; leaflets 9–31, serrate; staminate flowers short-stalked, with round receptacle and 7–85(–105) stamens; nut 4-celled at the base, falsely 5-celled at the apex; pistillate spike 2- to 5-(to 10-)flowered; embryo and seedling with 5 rows of scales, these merging into small spirally arranged compound leaves; top of leaf scar without hairy fringe.

TYPE: *J. nigra* L.
Sixteen species, North, Central, and South America and the West Indies.

Sect. c. **Cardiocaryon** Dode, Bull. Soc. Dendrol. France 11: 22. 1909.

Husk indehiscent, persistently attached to the nut; nut rough-ridged (though smooth in one cultivated variety), with 4 or 8 ridges, these in some cases represented by lines, with rugosities between the ridges; leaflets 9–17, serrate; staminate flowers sessile, the receptacle elongate with 7–18(–25) stamens; pistillate spike elongate with 5–10(–25) flowers; nut 2-celled at the base, 1-celled at the apex; embryo and seedling with 5 rows of scales, these merging into small alternate compound leaves; top of leaf scar notched with hairy fringe.

TYPE: *J. sieboldiana* Maxim. = *J. ailantifolia* Carr.
Three species; Japan, Manchuria, eastern China, Taiwan.

Sect. d. **Trachycaryon** Dode ex. Mann.

Juglans sect. *Trachycaryon* Dode, Bull. Soc. Dendrol. France 11: 22. 1909. nom.
Juglans sect. *Cinerea-Regia*, subsect. *Cinnerea* Nagel, Bot. Jahrb. Syst. 50: 482. 1914. LECTOTYPE: *J. cinerea* L.

Exocarpium indehiscens; endocarpium, id est nux vere, valde et argute poratum, porcis 8 vulgo prominentibus; flores staminati sessiles, receptaculis elongatis; nux basin bilocularis; embryo et plantula sine squamis; caulis plantulae elongatus, pro maxima parte aphyllus, supra foliae compositae ferens.

Husk indehiscent; nut strongly and sharply ridged, 8 of the ridges usually prominent with sharp anastomosing cross ridges; leaflets 11–19, serrate; staminate flowers sessile, the receptacle elongate with 7–15 stamens; pistillate spike 5- to

8-flowered; nut 2-celled at the base, 1-celled at the apex; embryo and seedling without scale leaves beyond the 2 or 3 buds superposed above the cotyledons, the rather large compound leaves appearing on the seedling above a long naked area of the stem; top of leaf scar not notched, with hairy fringe.

TYPE: and only species, *J. cinerea* L.
Eastern United States.

3. **Pterocarya** Kunth, Ann. Sci. Nat. (Paris) 2: 345. 1824.

Cyclocarya Iljinsk., Trudy Bot. Inst. Akad. Nauk SSSR, Ser. 1, Fl. Sist. Vyss. Rast. 10: 115. 1953. TYPE: *P. paliurus* Batal.

Deciduous trees; pith chambered; buds stalked, the terminal bud prominent, the lateral often superposed; buds naked or, if scaly at first, naked in late autumn; leaves exstipulate, odd-pinnate, though terminal leaflet sometimes reduced; leaflets serrate, glandular-dotted beneath; plants monoecious; staminate catkins short-stalked, lateral, solitary or in clusters of 3–5, in the axils of leaf scars or of the scars of scale leaves on old wood, or in the axils of bud scale scars at the base of new growth; immature staminate catkins (naked catkin buds) present on old wood in winter, or when bud scales are present, hidden within the bud scales in late summer and appearing at the base of the immature leaves of the bud in late autumn after the bud scales have fallen off; pistillate catkins 10- to many-flowered, finally drooping, terminal on new growth; staminate and pistillate flowers with bract and 2 bracteoles and 4 sepals, the sepals in the staminate flowers often reduced in number; bract small, narrow, unlobed; staminate flowers consisting of 9–31 stamens apparently located on the bract, bracteoles, and sepals, as these are fused with the floral receptacle; anthers glabrous or rarely slightly pubescent; apparent pistillate flower consisting of the bract, 2 bracteoles and 4 sepals, the sepals fused with the ovary to its tip, thus ovary inferior, the bract almost free from the ovary at its base, and the bracteoles almost free in the abaxial region (above the bract) but fused variously with the adaxial part of the ovary; carpels typically 2, median, or sometimes in individual flowers oblique or even transverse; style with 2 elongate recurved stigmatic style branches, the stigmatic areas on the inner surfaces of the style arms (carpels occasionally 3 on individual flowers of a spike); stigmas carinal, hence also typically median; fruit a small broadly winged nutlet, the 2 lateral wings or the completely circular one derived either from the 2 bracteoles alone or from the bracteoles and also in very small part from the bract when there is only one wing; the bract either a small scale at the base of nutlet or the scalelike tip of the bract appearing at the outer margin of the circular wing, this scale often disappearing; nutlet 2- or 4-celled at the base, usually with small lacunae in the wall; cotyledons entangled in the nutlet, in germination epigeal, appearing as small 4-lobed leaves, the next leaves simple or compound; cotyledonary node 1-gap 2-trace.

TYPE: *Juglans pterocarpa* Michx. = *P. fraxinifolia* (Lam. ex Poir.) Spach.
Six species, Caucasus Mts. of USSR, Iran, Japan, China, Laos and Viet Nam.

Subgen. 1. **Pterocarya.**

Pterocarya Kunth sensu Iljinsk., Trudy Bot. Inst. Akad. Nauk SSSR, Ser. 1, Fl. Sist. Vyss. Rast. 10: 38. 1953. TYPE: *Juglans pterocarpa* Michx. [*Pterocarya pterocarpa* (Michx.) Kunth ex Iljinsk.] = *P. fraxinifolia* (Lam. ex Poir.) Spach.

Buds naked, or if scaly at first becoming naked in late autumn; wood tending to be diffuse-porous; leaflet venation with none of lateral veins going directly to the teeth; staminate catkins solitary, short-stalked, in the axils of leaf scars or scars of scale-leaves on old wood, or in the axils of bud scale scars at the base of new growth; staminate flowers sessile, with elongate receptacle, 5–17 stamens, and the bracteoles slightly different in appearance from sepals, the whole flower zygomorphic; pollen grains (4-) 5- to 6-(to 8-) porate; pistillate flowers 40 or more per inflorescence, sessile, the bract fused only with the base of the ovary, separate from the 2 bracteoles, the latter unequally fused with the ovary, abaxially fused only with the base, adaxially fused to the base, the middle, or almost to tip of the ovary; nutlet 4-celled at the base, sessile, with 2 lateral separate broad wings derived exclusively from the bracteoles; bract remaining at the base of the nutlet as a small scale.

TYPE: *P. fraxinifolia* (Lam. ex Poir.) Spach [*P. pterocarpa* (Michx.) Kunth ex Iljinsk.].

Sect. a. **Pterocarya.**

Pterocarya sect. *Diptera* Henry in Elwes & Henry, Trees Gt. Brit. Irel. 2: 437. 1907; emend. Leroy, Mém. Mus. Natl. Hist. Nat., Sér. B, Bot. 6: 86. 1955. LECTOTYPE: *P. caucasica* Meyer = *P. fraxinifolia* (Lam. ex Poir.) Spach.

Pterocarya sect. *Stenoptera* Nagel, Bot. Jahrb. Syst. 50: 479. 1914. TYPE: *P. stenoptera* C. DC.

Pterocarya sect. *Eupterocarya* Rehder & Wilson in Sarg., Pl. Wils. 3: 181. 1916, emend. Iljinsk., Trudy Bot. Inst. Akad. Nauk SSSR, Ser. 1, Fl. Sist. Vyss. Rast. 10: 40. 1953. LECTOTYPE by Iljinskaya: *P. pterocarpa* (Michx.) Kunth ex Iljinsk., but this species not mentioned by Rehder & Wilson, so lectotype *P. stenoptera* C. DC.

Buds naked; lateral buds superposed; new growth not constricted at the base, without a ring of narrow bud scale scars at its base; staminate catkins solitary on old wood, in the axils of leaf scars or the scars of scale leaves; immature staminate catkins, naked catkin buds, appearing in late summer and persisting over winter as small budlike structures; stamens 5–17; bracts of staminate flowers, pistillate flowers, and fruits short, glabrous or with a few hairs; tips of the leaflets without tufts of hairs; nutlet usually with large cavities in the wall.

TYPE: *P. fraxinifolia* (Lam. ex Poir.) Spach [*P. pterocarpa* (Michx.) Kunth ex Iljinsk.].

Three species, Caucasus Mts. of USSR; Iran; eastern China, Laos, and Viet Nam.

Sect. b. **Platyptera** Nagel, Bot. Jahrb. Syst. 50: 481. 1914; emend. Rehder, Bibl. Cult. Trees and Shrubs: 89. 1949.

Pterocarya sect. *Chlaenopterocarya* Rehder & Wilson in Sarg., Pl. Wils. 3: 183. 1916. TYPE: *P. rhoifolia* Sieb. & Zucc.

Buds long, clearly stalked, conical, beaked, covered by a few hoodlike bud scales, these falling off in late autumn and then buds naked; lateral buds not superposed; new growth constricted at its base, with a ring of narrow bud scale scars at its base; staminate catkins solitary, at the base of new growth, essentially in a ring in the axils of bud scale scars, the immature catkins formed in late summer but not evident until late autumn after the bud scales have fallen off; bracts of staminate flowers, pistillate flowers, and fruits narrow, strongly hairy; stamens 9–13; tips of the leaflets with tufts of hairs, these sometimes deciduous; nutlets without cavities in the wall.

LECTOTYPE: *P. rhoifolia* Sieb. & Zucc. in Rehder, Bibl. Cult. Trees and Shrubs: 89, 1949, indicated by synonymy of sect. *Chlaenopterocarya* Rehder & Wilson.

Two species, western China, Tibet, and Japan.

Subgen. 2. **Cyclocarya** (Iljinsk.) Mann., Bull. Torrey Bot. Club 102: 165. 1975.

Pterocarya sect. *Cycloptera* Franch., J. Bot. (Morot) 12: 318. 1898. TYPE: *P. paliurus* Batal.
Cyclocarya Iljinsk., Trudy Bot. Inst. Akad. Nauk SSSR, Ser. 1, Fl. Sist. Vyš. Rast. 10: 115. 1953. TYPE: *P. paliurus* Batal.

Buds naked; wood tending to be ring-porous; leaflet venation usually with some of the lateral veins going directly to the teeth; staminate catkins in clusters of 3–5, the clusters stalked, in the axils of leaf scars on old wood; staminate flowers short-stalked, with round receptacle, 20–31 stamens, and the 2 bracteoles similar to the usually 2 sepals, the flower appearing actinomorphic; pollen grains 3- to 4-(to 7-)porate; pistillate flowers 10–20, short-stalked, the base of the bract fused with the 2 bracteoles, the involucre in turn fused equally with the base of the ovary or the middle(?); nutlet 2-celled at the base, short-stalked, with one circular wing derived mostly from the bracteoles but also in very small part from the bract; bract not at the base of nutlet, but the tip of the bract remaining as a small often deciduous scale at the outer margin of the wing of the fruit.

TYPE: and only species, *P. paliurus* Batal.

Eastern China.

I believe that *Pterocarya* is closely related to *Juglans*, not so closely to *Platycarya* or to *Engelhardia*; the relationship to the last two genera is indicated by the classifications of various authors.

The relationship of *Pterocarya* to *Juglans* is indicated in the key to genera and the descriptions of the tribes. The pith is chambered in both genera, and there is a similar organization of the type and positions of staminate inflorescences, the parts of the floral envelope present, the orientation of carpels, and the type and orientation of stigmas. The wood anatomy, according to Kribs (1927) and Heimsch & Wetmore (1939), is extremely close; and there is a clear evolutionary development of the types of pollen grains from *Pterocarya* to *Juglans* (Whitehead, 1963, 1965; Stone & Broome, 1975); see Fig. 1. Although there is some relationship of *Pterocarya* to *Engelhardia*, as presumably the two genera had a common ancestor, the type of bracts and stigmas, and the positions

and types of inflorescences are quite different. The similarity of small-winged fruits, wth the involucre at a low position on the ovary, is superficial. See Stone (1973) for a discussion of the relationships of the fruits of the family.

TRIBE B. ENGELHARDIEAE Mann., stat. nov.

Tribe(?) Engelhardtieae Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbhavn 1870a: 172, 1870b: 2. LECTOTYPE: *Engelhardia* Lesch. ex Blume.
Tribe Alfaroeae Koidzumi, Acta Phytotax. Geobot. 6: 10. 1937. TYPE: *Alfaroa* Standl.

Pith solid; buds naked; leaves alternate, opposite or rarely whorled, even-pinnate; leaflets serrate or entire; staminate and pistillate inflorescences in the same position (axillary or terminal) in a given species, frequently combined into an androgynous panicle; staminate catkins clustered, elongate, drooping; pistillate catkin many-flowered, elongate, finally pendulous; bract broad, 3-lobed in staminate and pistillate flowers, the lobes rarely filiform; staminate flower consisting of 3-lobed bract, 2 bracteoles (or these very rarely absent), 4 to 1 (or rarely 0) sepals, and 4–23 stamens; pistillate flower consisting of 3-lobed bract and 2 bracteoles fused with the base of the ovary, and 4 sepals fused to its tip; bract modified into a large anterior 3-lobed wing for the fruit, or in one genus reduced to a minute scale at base of the fruit; bracteoles adaxial, varying in flower from a prominent 2-lobed structure to a minute line around the base of the ovary, and in fruit from a large adaxial 2-lobed wing to apparently no structure; carpels median; style present or absent, stigmas carinal, commissural or split-carinal; fruit a small to medium winged nutlet, or a thin- to thick-skinned nut without a wing or true husk; shell of nutlet and nut cartilaginous-subligneous, rather thin; septa thin; fruit 2- to 4- to 8-celled near the base; pericarp without lacunae; cotyledons hypogeal or epigeal in germination.

TYPE: *Engelhardia* Lesch. ex Blume.

4. **Engelhardia** Lesch. ex Blume, Bijdr. 10: 528. 1825.

Pterilema Reinw., Syll. 2: 13. 1826. TYPE: *P. aceriflorum* Reinw. = *E. spicata* Lesch. ex Blume var. *aceriflora* (Reinw.) Koord. & Valet.

Deciduous or sometimes evergreen trees; pith solid; buds naked; leaves exstipulate, alternate, even-pinnate, the leaflets serrate or entire, glandular-dotted beneath; leaflet venation, intercostal mesh with free-ending veinlets; large rhombic leaflet crystals absent; trees monoecious or dioecious; staminate and pistillate inflorescences separate or combined in an androgynous panicle, the pistillate central; all catkins elongate, pendulous; staminate and pistillate inflorescences in the same location in a given species, either terminal on new growth or lateral on old wood; staminate catkins in clusters of 3–6; bract broad, 3-lobed in all flowers, sometimes much enlarged in staminate flowers; 2 bracteoles and 4 sepals present in both staminate and pistillate flowers, though sepals often reduced in number in the former or even absent; stamens 4–13; anthers pubescent or glabrous; pollen diameter averaging (13–)15–19(–25) μm; polar view of pollen oblate to oblate-spherical; involucre fused with the lower half of the ovary and the sepals fused to the top; carpels median; stigmas either commissural, the

stigmatic areas on the edges of the elongate style arms, and the stigmatic style arms transverse (lateral), or the style absent and the stigmas short on the top of the ovary, split-carinal; fruit a small nutlet, with a large 3-lobed anterior wing derived from the development of the bract, the bracteoles present as a much reduced often 2-lobed adaxial wing; large central lobe of the wing of the bract pinnately veined; fruit with thin skin, developed from calyx; nutshell cartilaginous-subligneous, rather thin, without lacunae; septa of the fruit thin, the fruit mostly 4-celled at the base due to a primary partition and a low secondary one, possibly 2-celled in smaller fruits; cotyledons entangled in the seed, the testa loose in fruit; cotyledons epigeal in germination, first true leaves of the seedling simple or compound; cotyledonary node 1-gap, 2-trace.

LECTOTYPE: *E. spicata* Lesch. ex Blume.

Five species, northern India to eastern China, Indo-China, East Indies, and Philippines.

Sect. a. **Engelhardia**.

Engelhardia sect. *Pterilema* (Reinw.) C. DC., Ann. Sci. Nat. Bot. Sér. 4, 18: 35. 1862. TYPE: *E. aceriflora* (Reinw.) Blume = *E. spicata* Lesch. ex Blume var. *aceriflora* (Reinw.) Koord. & Valet.

Engelhardia sect. *Trichotocarpeae* Nagel, Bot. Jahrb. Syst. 50: 475. 1914. LECTOTYPE: *E. spicata* Lesch. ex Blume.

Leaves deciduous or evergreen; inflorescences lateral on old wood; staminate flower sessile, the receptacle elongate; calyx usually irregular, the sepals often reduced in number or rarely even absent; stamens 4–13, the anthers pubescent; pistillate flower essentially sessile; style present, short; stigmas elongate, commissural, stigmatic areas on the edges of each style arm, or sometimes the style arms split so there are 4 elongate filiform stigmas; fruit sessile or obscurely short-stalked, 4-celled at the base in most fruits, possibly 2-celled in smaller ones; body of fruit and lower part of bract hairy.

TYPE: *E. spicata* Lesch. ex Blume.

Four species, northern India to eastern China, Malaya, East Indies to Philippines.

Sect. b. **Psilocarpeae** Nagel, Bot. Jahrb. Syst. 50: 475. 1914, emended Leroy, Mém. Mus. Natl. Hist. Nat., Sér. B, Bot. 6: 126. 1955.

Leaves apparently evergreen; inflorescences terminal; staminate flower short-stalked, the receptacle round, the perianth cup-shaped, regular in appearance, typically of 4 similar organs (2 bracteoles and 2 sepals?); stamens 4–12; anthers glabrous; pollen diameter averaging 15(13–17) μm; exine thick; pistillate flower and fruit clearly short-stalked to long-stalked (7 mm long); style absent, the stigmas short, on top of the ovary, split-carinal; body of fruit and bract glabrous though usually densely glandular dotted; fruit 4-celled at the base.

LECTOTYPE: (by Leroy) *E. wallichiana* Lindl. ex C. DC. = *E. roxburghiana* Wall.

East Pakistan, southern China, Taiwan, Viet Nam, Borneo, Sumatra.

Engelhardia, *Oreomunnea*, and *Alfaroa* are very closely related in having similar broad 3-lobed bracts, inflorescence position and type, floral envelopes, leaflet pinnation, buds, pith, wood anatomy, and pollen. Manning (1966) suggested that the 3 genera could essentially be considered one genus. Crepet et al. (1975) and Dilcher et al. (1976) show that an almost identical 3-lobed bract occurred in ancestral genera in the Eocene. The two American genera are quite different in arrangement of leaves, cross section of the fruit, and germination of the fruit, but the relationship otherwise is very close. *Alfaroa* clearly should not be placed in the same tribe as *Juglans* and *Carya*. The relationship of the group to *Pterocarya* is discussed under that genus. All studies indicate that the three genera as a whole are the most primitive in the family.

5. **Oreomunnea** Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøhavn 1856: 33.

Engelhardia sect. *Oreomunnea* (Oerst.) C. DC., Ann. Sci. Nat. Bot. sér. 4, 18: 32. 1862.
TYPE: *O. pterocarpa* Oerst.

Evergreen trees; pith solid; buds naked, the lateral superposed; leaves exstipulate, opposite, even-pinnate; leaflets 4–12, glandular-dotted beneath, serrate or entire on young trees, entire on mature ones; leaflet venation, intercostal mesh with closed veinlets; plants monoecious; staminate panicles of catkins separate or combined with a central pistillate spike to form an androgynous panicle; inflorescences terminal or lateral, all catkins many-flowered, drooping; bract broad, 3-lobed in staminate and pistillate flowers; 2 bracteoles and 4 sepals present in both flowers but sepals often reduced in staminate flowers; staminate flowers sessile, the receptacle round or elongate, with 3-lobed bract, 2 bracteoles, 1–4 sepals and 8–23 stamens; anthers glabrous; pollen diameter averaging 21 μm (19–23); polar view subtriangular, equatorial view sublobate; pistillate flowers short-stalked; involucre fused with the lower half of the ovary, and the 4 sepals fused to the top; 6 sepals found in one 3-carpelled fruit of *O. pterocarpa*; carpels median, the stigmatic areas short, subglobose or horseshoe shaped at the tips of the elongate style arms; fruit a short-stalked nutlet, medium in size, with a large anterior 3-lobed wing from the development of the bract, but with a smaller 2-lobed rather prominent posterior wing developed from the 2 bracteoles; fruit with subligneous rather thin wall, covered by a thin skin developed from the sepals, with thin septa, 8-celled in the middle, the primary and secondary partial partitions and tertiaries with projections into the loculus so in part more than 8-celled; lacunae absent in the walls; central lobe of the fruit wing trinerved; cotyledons separate, not entangled in the fruit, one to a valve, hypogeal in germination; first true leaves of seedling simple; cotyledonary node 1-gap, 3-trace; fruit and wings both larger than those of *Engelhardia* of Asia.

TYPE: *O. pterocarpa* Oersted.
Two species, Mexico and Central America.

6. **Alfaroa** Standl., J. Wash. Acad. Sci. 17: 77. 1927.

Evergreen trees; pith solid; buds naked; leaves exstipulate, opposite or

whorled, rarely in part alternate, even-pinnate; leaflets 4–12, glandular-dotted beneath, serrate on young trees, entire on mature ones; leaflet venation, intercostal mesh with closed veinlets; plants monoecious; staminate panicles of catkins separate or combined with a central pistillate spike to form an androgynous panicle; inflorescences terminal or lateral, all catkins many-flowered, drooping; bract broad, 3-lobed in staminate and pistillate flowers; 2 bracteoles and 4 sepals present in both flowers but sepals often reduced in staminate ones; staminate flowers sessile, the receptacle round or elongate, with a 3-lobed bract, 2 bracteoles, 1–4 sepals and 6–10 stamens; anthers glabrous; pollen diameter averaging 24 μm; polar view subtriangular, equatorial view sublobate; pistillate flowers sessile, the 3-lobed bract very small, fused only with the very base of the ovary, and not enlarging into a wing for the fruit but remaining as a minute scale at the base of the fruit; sepals fused to the top of the ovary; carpels median, the stigmatic areas short, subglobose or horseshoe shaped at the tips of the elongate style arms; bract so small that the venation is not recognizable in pistillate flower or fruit; bracteoles (adaxial) so small that these are essentially absent; fruit a rather large thin- to thick-skinned nut compared with the medium size of *Oreomunnea*, not winged nor with a true husk (that is, not developed from the involucre); wall of nut thin to thick, subligneous, covered with a thin to thick skin developed from the calyx, with thin septa, 8-celled in the middle, the primary and secondary partial partitions and tertiaries with projections into the loculus so in part more than 8-celled; lacunae absent in the walls; cotyledons separate, not entangled in the fruit, 1 to a valve, hypogeal in germination; first true leaves of seedling simple or compound; cotyledonary node 1-gap, 3-trace.

TYPE: *A. costaricensis* Standl.

Seven species, Mexico, Central America, and northwestern South America (Colombia).

TRIBE C. HICORIEAE Mann., nom. nov.

Tribe Caryeae Koidzumi, Acta Phytotax. Geobot. 6: 10. 1937, excl. *Juglans* L., nom. superfl. (incl. *Juglans* Linnaeus).

Pith solid; bud scales present, sometimes accrescent in spring; leaves exstipulate, alternate, odd-pinnate; leaflets 3–17, glandular-dotted beneath, serrate or entire; unlobed bract and the bracteoles both rather broad in the pistillate flower, developing in the fruit into a husk which is completely or partially 4- to 6-valved at maturity; bracteoles apparently 3–5, but these may represent 2 bracteoles, variously lobed and divided, though the posterior 1–3 sometimes interpreted as sepals; plants monoecious; staminate and pistillate inflorescences in different locations, the pistillate terminal and few-flowered, the staminate in clusters of 3–8, lateral at the base of new growth, drooping; bracteoles present in the staminate flower; sepals normally absent in the staminate and pistillate flowers, though 1 or 2 sepals occasionally present in individual staminate flowers, and sepals possibly represented in the pistillate ones by the 4-lobed stigmatic disk below the stigmas and apparently confluent with them; carpels transverse; common style apparently absent; stigmas commissural, thick, hence apparently

median, rather short, the stigmatic area completely covering the style branches and stigmatic disc (when present); style branches occasionally split so 4 stigmas present; fruit large, consisting of a nut enclosed in a completely or incompletely 4- to 6-valved husk; nut shell woody, externally smooth, often 4-angled, rarely somewhat wrinkled, often with lacunae present in the wall; nut 2- to 4-celled at the base; cotyledon 1 in each valve (not carpel), fleshy; germination hypogeal.

TYPE: *Carya* Nutt., the only genus.

7. *Carya* Nutt., Gen. N. Amer. Pl. 2: 220. 1818, nom. cons.

Hicorius Raf., Fl. Ludovic.: 109. 1817, nom. rejic. LECTOTYPE: *H. amara* (Michx.) Raf.
Hicoria Raf., Alsogr. Am. 65. 1838, orth. mut. TYPE: *Juglans alba* L. (fide Britton, N. Amer. Trees, 223.)
Pacania (Raf.) Dochnahl, Sich. Fuhr. Obstk. 4: 26. 1860. TYPE: *Hicoria oliveformis* Raf.

Deciduous (or rarely evergreen?) trees; pith solid (or rarely hollow?); bud scales present; terminal bud prominent, the lateral buds often superposed; leaves exstipulate, alternate, odd-pinnate; leaflets glandular-dotted beneath, serrate or entire; flowers appearing with the leaves; staminate flowers in axillary drooping catkins, these in stalked clusters of 3–8, each flower in the axil of a bract and 2 bracteoles; sepals typically absent, but 1 or 2 rarely present in individual flowers of a catkin of some species; stamens 3–15, usually 4; anthers pubescent; pistillate flowers sessile, in terminal 2- to 10-flowered spikes, consisting of a 1-celled ovary enclosed by an apparently 4- to 6-lobed involucre (bract and 3–5 bracteoles or bract and 2 bracteoles, the latter variously lobed at the apex); (a ring of 2–3 "sepals" reported as occurring occasionally inside the involucral ring in a few species); carpels transverse; stigmas 2, short, commissural (hence median), these frequently each 2-parted, a stigmatic disc (modified calyx?) usually beneath the stigmas; fruit a nut enclosed in an adherent husk, the whole globose to oblong, the husk separating more or less completely into 4–6 valves, and typically becoming free from the nut at maturity; nut smooth or slightly rugose, often angled. 2- to 4-celled at the base, 1-celled at the apex; cotyledons fleshy, not entangled in the nut, hypogeal at germination; cotyledonary node 3- to 6-gap, 3- to 6-trace.

LECTOTYPE: *C. tomentosa* (Lamarck) Nuttall (*Juglans alba* Linnaeus in part).
Seventeen species, eastern United States, northeastern Mexico, eastern Asia.

Sect. a. **Carya.**

Hicoria subgen. *Glycaria* Raf., Alsogr. Am. 66. 1838. TYPE: *Hicoria alba* (L.) Raf.
Hicoria subgen. *Hexacaria* Raf., Alsogr. Am. 66. 1838. TYPE: *H. tomentosa* Raf.
Hicoria sect. *Euhicoria* Dippel, Handb. Laubh. 2: 331. 1892. LECTOTYPE: *H. alba* (L.) Britt.
Carya sect. *Eucarya* C. DC., Prodr. 16, 2: 142. 1864. LECTOTYPE: *C. tomentosa* Nutt.
Hicoria sect. *Eucarya* (C. DC.) Sarg., Sylva N. Amer. 7: 135. 1895. LECTOTYPE: *C. tomentosa* Nutt.

Pith solid; bud scales 6–12, imbricated, strongly accrescent in spring; leaflets 3–9, serrate, not falcate; staminate catkins essentially in a ring around the stem, in the axils of early deciduous bud scales (or rarely also in the axils of 1 or 2 leaves above the bud scale zone) at the base of elongate leafy growth, in clusters of 3 (very rarely of 4, 5, 6 or 7 in individual trees); stamens 3–8(–10?), usually 4;

bracteoles in pistillate flower in addition to bract apparently 3, rarely 2 or 4; stigmatic disc present beneath the true stigmas; husk 4-valved, rarely in individual trees 3- or 5-valved, the valves not keeled nor usually winged along the margins; nut shell rather thick, without definite lacunae; secondary septa well developed, hence nut 4-celled below; secondary internal ridges (projections) present and often tertiary ones also; outer common ring of involucral and carpellary vascular bundles ascending in the outer or inner part of the primary partition; first true leaf above several spiral scale leaves of seedling usually slightly lobed, the second leaf compound with 3 leaflets; $n = 16$ or $n = 32$.

TYPE: *C. tomentosa* Nutt.

Eight species, eastern United States to northeast Mexico.

Sect. b. **Apocarya** C. DC., Prodr. 16, 2: 144. 1864.

Hicoria subgen. *Pacania* Raf., Alsogr. Am. 65. 1838. TYPE: *H. oliveformis* Raf.
Hicoria subgen. *Drimocaria* Raf., Alsogr. Am. 66. 1838. TYPE: *H. amara* Raf.
Hicoria sect. *Apohicoria* Dippel, Handb. Laubh. 2: 336. 1892. LECTOTYPE: *H. minima* Britton.
Carya sect. *Pacania* (Raf.) Rehder, J. Arnold Arbor. 28: ined. 1947, see Rehder, Bibl. Cult. Trees and Shrubs: 91. 1949. TYPE: *Hicoria oliveformis* Raf.

Pith solid; bud scales few, 4–6, valvate, not accrescent in spring or only slightly so, the buds possibly naked in the Chinese species, *C. cathayensis*; leaflets 5–17, serrate, commonly falcate; staminate catkins in clusters of 3, essentially in a ring around the stem in the axils of early deciduous bud scales, these located at the base of long terminal leafy shoots, or in most species some or all of them usually on short special essentially leafless side branches attached to old wood in the axils of leaf scars; stamens 3–8, usually 4; in pistillate flowers bracteoles in addition to bract commonly 3, rarely 2, 4, or 5; beak of ovary absent, though nut pointed; stigmatic disc present; husk 4-, rarely 3-, 5- or 6-valved, the segments (valves) not keeled, frequently winged along the margins; nut shell thin, rarely thick; nut with lacunae present in the wall (in the internal ridges and sometimes at the ends of the primary partition) in most but not all species; secondary septa present or reduced to a pair of wings from the primary partition and appearing absent, hence nut 2- to typically 4-celled below; secondary and tertiary internal ridges usually present; outer common ring of involucral and carpellary vascular bundles ascending in outer or inner part of primary partition; first true leaves above several alternate scale leaves of seedling mostly simple, unlobed, or in *C. myristiciformis* one slightly lobed leaf followed by a compound leaf with 3 leaflets; $n = 16$.

LECTOTYPE: *C. oliveformis* (Raf.) Nutt. = *C. illinoensis* (Wang.) K. Koch.

Five species, northeastern United States to northern Mexico; 3 species eastern China to northern Viet Nam and eastern India (eastern Pakistan).

Sect. c. **Rhamphocarya** (Kuang) Mann. & Hjelmqvist, Bot. Not. 1951, 4: 330. 1951.

Annamocarya Chev., Rev. Int. Bot. Appl. Agric. Trop. 21: 504. 1941. TYPE: *A. indochinensis* Chev. = *Carya sinensis* Dode.

Rhamphocarya Kuang, Icon. Fl. Sin. 1: 1. 1941. TYPE: *R. integrifoliolata* Kuang = *C. sinensis* Dode.

Pith hollow or solid; bud scales few, unequal; leaflets 7–9, entire, not falcate; staminate catkins much elongated, in clusters of 5–8 at the base of elongate leafy shoots, apparently scattered along the base of the shoot rather than in a close ring, evidently in the axils of lower foliage leaves; stamens 5–15; pistillate flowers with 3–5 bracteoles in addition to the bract, the ovary with a beak so the stigmas not strictly sessile; stigmatic disc apparently absent; husk 4- to 6-valved, the valves typically keeled, at least above; nut apiculate; lacunae absent in the wall of the nut in the lower part but sometimes present near the apex; secondary partition weakly developed, represented by a pair of wings from the primary partition hence the nut essentially 2-celled at the very base; secondary internal ridges present but tertiary ones apparently absent; cavity in nut large at the apex; outer common ring of involucral and carpellary vascular bundles ascending in the potential nut-shell part of the ovary wall; nature of leaves of seedling unknown.

TYPE: and only species, *C. sinensis* Dode.
Southern China and northern Viet Nam.

The mature fruit of *Carya* with its thick husk is quite similar to that of *Juglans*, and the husk of *J. regia* is irregularly 4-valved much as in *Carya*. Furthermore, the general, but not the detailed, arrangement of inflorescences is similar in the two genera. The location of lacunae in the nuts of *Carya* is for the most part rather different from that of *Juglans*, but Leroy (1955) points out that *C. poilanei* shows an intermediate condition. Leroy (1955: 82) believes that there is an evolutionary series of development in arrangement of vascular bundles of the carpels in the flower and fruit from *Annamocarya* (*Carya*, sect. *Rhamphocarya*) through certain species of *Carya* to *Juglans*. Thus practically all writers have placed *Juglans* and *Carya* in the same tribe. However, the two are different in the parts of the floral envelope present in both staminate and pistillate flowers, the location of staminate inflorescences, orientation of carpels, type and orientation of stigmas, anatomy of the wood, and the type of pollen grains. Furthermore, the pith in *Carya* is solid, not chambered. With reference to the floral anatomy as discussed by Leroy, it should be pointed out that the floral anatomy of the carpels of *Juglans* is very close to that of *Pterocarya* and of *Engelhardia*, and the primitive condition, according to Leroy, of *Annamocarya* is quite different from that of the truly primitive condition of *Engelhardia* (from which presumably *Carya* probably evolved). Thus *Carya* and *Juglans* have followed a parallel evolutionary development; Stone (1973) has discussed the evolutionary development of the fruits in the family. Studies of wood anatomy and of pollen grains indicate that *Carya* is not only along a different line of evolution, but is the most advanced genus in the family. I have placed the genus in a separate tribe.

Four species of *Carya* have been reported to be tetraploid, *C. glabra*, *C. ovalis*, *C. floridana*, *C. texana*, *C. pallida*, *C. tomentosa*; $n = 32$.

TABLE 3. List of species of Juglandaceae arranged according to the classification in this paper, with general distribution of each species.

SUBFAM. I. PLATYCARYOIDEAE Mann.		
1. *Platycarya* Sieb. & Zucc.	1 sp.	
P. strobilacea Sieb. & Zucc.		Korea, eastern China, Viet Nam, Japan
SUBFAM. II. JUGLANDOIDEAE		
TRIBE A. JUGLANDEAE		
2. *Juglans* L.	21 spp.	
Sect. a. *Juglans*		
J. regia L.		southeastern Europe, Iran to Himalayas, and China
subsp. *turcomanica* Popov		
subsp. *fallax* (Dode) Popov		
Sect. b. *Rhysocaryon* Dode		
J. australis Griseb.		Argentina
J. boliviana (C. DC.) Dode		western South America
J. californica S. Wats.		California
J. hindsii (Jeps.) Rehder[3]		California
J. hirsuta Mann.		northeastern Mexico
J. jamaicensis C. DC.[2]		West Indies
J. major (Torr. ex Sitsgr.) Heller		
var. *major*		southwestern United States, northwestern Mexico
var. *glabrata* Mann.[1]		south-central Mexico
J. microcarpa Berl.		
var. *microcarpa*		southwestern United States, northwestern Mexico
var. *stewartii* (Johnston) Mann.[3]		northern Mexico
J. mollis Engelm. ex Hemsl.		central Mexico
J. neotropica Diels		northwestern South America
J. nigra L.		eastern United States
J. olanchana Standl. & L. O. Williams[2]		
var. *olanchana*[3]		Guatemala
var. *standleyi* Mann.[3]		southwestern Mexico
J. pyriformis Liebm.		southeastern Mexico
J. soratensis Mann.[4]		Bolivia
J. steyermarkii Mann.		Guatemala
J. venezuelensis Mann.[2]		Venezuela
Sect. c. *Cardiocaryon* Dode		
J. ailantifolia Carr.		
var. *ailantifolia*		Japan
var. *cordiformis* (Makino) Rehd.[3]		Japan
J. cathayensis Dode		eastern China, Taiwan
J. mandshurica Maxim.		Manchuria, northeastern China, Korea
Sect. d. *Trachycaryon* Dode ex Mann.		
J. cinerea L.		eastern United States
3. *Pterocarya* Kunth	6 spp.	
Subgen. *Pterocarya*		

TABLE 3. Continued

Sect. a. *Pterocarya*	
P. fraxinifolia (Lam. ex. Poir.) Spach	USSR Caucasus, Iran
P. hupehensis Skan.	eastern China
P. stenoptera C. DC.	
var. *stenoptera*	eastern China, Viet Nam, Laos
var. *tonkinensis* Franch.[3]	Viet Nam
Sect. b. *Platyptera* Nagel emend. Rehder	
P. rhoifolia Sieb. & Zucc.	Japan
P. macroptera Batal.	
var. *macroptera*[1]	northwestern China
var. *delavayi* (Franch.) Mann.[1]	western China
var. *forrestii* (W. W. Smith ex Hand.-Mazz.) Mann.[1]	western China, Tibet
var. *insignis* (Rehder & Willson) Mann.[1]	western China
Subgen. 2. *Cyclocarya* (Iljinsk.) Mann.	
P. paliurus Batal.	eastern China
TRIBE B. ENGELHARDIEAE Mann.	
4. *Engelhardia* Lesch. ex Blume	5 spp.
Sect. a. *Engelhardia*	
E. apoensis Elmer ex Nagel	Malaya, Borneo, Philippines
E. rigidia Blume	
var. *rigida*	Java, Borneo, New Guinea
var. *subsimplicifolia* (Merr.) Mann.[1]	Borneo, New Guinea, Philippines
E. serrata Blume	
var. *serrata*	Malaya, Java, Philippines
var. *cambodica* Mann.[3]	southwestern China, Cambodia, Burma, Thailand
var. *nudiflora* (Hook.f.) Mann.[1]	Thailand, Malaya, Sumatra, Borneo
var. *parvifolia* (C. DC.) Mann.[1]	Sumatra, Borneo, Philippines
E. spicata Lesch. ex Blume	
var. *spicata*	Nepal, western India, southern China, Malaya, East Indies, Philippines
var. *aceriflora* (Reinw.) Koord. & Valet.	Tibet, northern India, Burma, Thailand, Java, New Guinea, Philippines
var. *colebrookeana* (Lindl. ex Wall.) K.&V.	northern India, western China, Burma, Laos, Thailand, Philippines
Sect. b. *Psilocarpeae* Nagel emend. Leroy	
E. roxburghina Wall.[2]	East Pakistan, southern China, Taiwan, Viet Nam, Sumatra, Borneo
5. *Oreomunnea* Oerst.	2 spp.
O. mexicana (Standl.) Leroy[2]	
subsp. *mexicana*	Mexico, Central America
subsp. *costaricensis* Stone[3]	Costa Rica
O. pterocarpa Oerst.[2]	Costa Rica
6. *Alfaroa* Standl.	7 spp.
A. costaricensis Standl.	Mexico to Panama
A. guanacastensis Stone[3]	Costa Rica

TABLE 3. Continued

	A. guatemalensis (Standl.) L. O. Williams[3]	Guatemala
	A. hondurensis L. O. Williams ex Mann.[4]	Honduras
	A. manningii León[3]	Costa Rica
	A. mexicana Stone[3]	eastern Mexico
	A. williamsii A. Molina[3]	
	subsp. *williamsii*[3]	Nicaragua
	subsp. *tapantiensis* Stone[3]	Costa Rica
TRIBE C. HICORIEAE Mann.		
7.	*Carya* Nutt.	17 spp.
	Sect. a. *Carya*	
	C. floridana Sarg.	Florida
	C. glabra (Mill.) Sweet	
	var. *glabra*	eastern United States
	var. *hirsuta* (Ashe) Ashe[3]	eastern United States
	var. *megacarpa* (Sarg.) Sarg.[3]	southeastern United States
	C. laciniosa (Michx.) Loud.	eastern United States
	C. ovalis (Wang.) Sarg.	
	var. *ovalis*	eastern United States
	var. *mollis* Ashe[3]	eastern United States
	C. ovata (Mill.) K. Koch	
	var. *ovata*	eastern United States
	var. *mexicana* (Engelm.) Mann.[1]	northeastern Mexico
	var. *australis* (Ashe) Little[3]	southeastern United States
	var. *pubescens* Sarg.[3]	eastern United States
	C. pallida (Ashe) Engl. & Graebn.	eastern United States
	C. texana Buckl.	
	var. *texana*	south-central United States
	var. *villosa* (Sarg.) Little	south-central United States
	C. tomentosa Nutt.	eastern United States
	Sect. b. *Apocarya* C. DC.	
	C. aquatica (Michx. f.) Laud.	southeastern United States
	C. cathayensis Sarg.	southeastern China
	C. cordiformis (Wang.) K. Koch	eastern United States
	C. illinoensis (Wang.) K. Koch	southeastern United States
	C. myristiciformis Nutt.	southeastern United States
	C. palmeri Mann.[3]	northeastern Mexico
	C. poilanei (Chev.) Leroy[3]	Laos, Viet Nam
	C. tonkinensis Lecomte	northeastern India, southern China, Viet Nam
	Sect. c. *Rhamphocarya* (Kuang) Mann. & Hjelmq.	
	C. sinensis Dode[2]	southeastern China, Viet Nam

Changes in names:

[1] Former species reduced to variety.
[2] Different specific name replacing former one or specific name removed to different genus.
[3] New species, subspecies, or variety described, or different name added.
[4] New species, but probably not a good species—hybrid?

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DICHANTHELIUM (POACEAE) IN THE UNITED STATES AND CANADA[1]

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ABSTRACT

This is a taxonomic revision of the grass genus *Dichanthelium* as represented in the United States and Canada. Keys and descriptions are provided for the 45 taxa (26 species and 19 varieties) of the United States and Canada recognized by the writers. A total of 26 new combinations and changes of status are proposed. Many species of the genus *Dichanthelium* (*Panicum* subgenus *Dichanthelium* Hitchc. & Chase) are widespread through the eastern half of the United States and the center of diversity appears to be in southeastern North America. At least some species are present almost throughout the cool, subtropical and tropical regions of North America and the Caribbean, and a few species range throughout much of South America. The genus also is represented in the Hawaiian Islands. This publication represents the first major revision of the *Dichanthelium* grass group since the monograph of *Panicum* by Hitchcock and Chase in 1910.

Linnaeus (1753), in *Species Plantarum*, described the first three species that are included in the *Dichanthelium* group, *Panicum dichotomum*, *P. clandestinum*, and *P. latifolium*. *Panicum dichotomum* L. was designated as the type species of *Panicum* subgenus *Dichanthelium* by Hitchcock & Chase (1910) and is herein accepted as the type of the genus *Dichanthelium*. Lamarck in 1798 described *Panicum scoparium*, *P. laxiflorum*, *P. nitidum*, and *P. nodiflorum*; the last two species are now submerged in synonymy under *Dichanthelium dichotomum*. Most of the subsequent naming of dichanthelia taxa was done by the following workers: Elliott 8, Vasey 14, Scribner 22, Ashe 48, Nash 44, and Hitchcock 15. Among the other early botanists who contributed names were Swartz, Pursh, Poiret, Schultes, Sprengel, Michaux, Kunth, Nees, Desvaux, A. Gray, Chapman, Trinius, Torrey, Steudel, Grisebach, and Fournier.

In 1885, in a catalogue of the grasses of the United States, George Vasey listed 12 species of rosette-forming panicums. Four years later, in the first monograph of *Panicum*, Vasey (1889) recognized 20 species and 18 varieties in this group. In *Grasses of North America*, Beal (1896), recognized only 13 species and 6 varieties. During the period 1893–1900, G. V. Nash and W. W. Ashe collected extensively throughout the Carolinas and Florida and named a total of 92 new rosette-forming panicums. In 1901 Scribner and Merrill prepared an annotated list of the New England species of *Panicum*, and in this list most of the species of Nash and Ashe were put in synonymy or retained as varieties.

[1] Technical article No. T.A. 14123, Texas Agricultural Experiment Station, College Station, Texas. This work was funded in part by NSF Grant No. DEB 75-06436. The authors are especially grateful to the curators of the herbaria of the Missouri Botanical Garden (MO), the New York Botanical Garden (NY), Texas A&M University (TAES), the University of Texas (TEX), and the Smithsonian Institution (US) for the use of specimens and loan of type material. Special thanks are due the graduate students, Robert B. Shaw, Kelly W. Allred, José Valls, and Michael Folsom for their assistance in various phases of the *Dichanthelium* project and to Judy L. Farnsworth for her general assistance in the preparation and typing of the manuscript.

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ANN. MISSOURI BOT. GARD. 65: 1088–1132. 1978.

0026-6433/78/1088–1132/$04.55/0

In the same year, Scribner (1901), in a comprehensive treatment of American grasses, recognized 43 species of dichanthelia.

In 1910 A. S. Hitchcock and Agnes Chase published their monumental treatment of the North American species of *Panicum*. Included were keys to the subgenera and the "groups" of subgenus *Dichanthelium*, species writeups with complete citation of synonyms and rejected species, morphological descriptions and numerous excellent spikelet illustrations, brief statements of habitat and distribution, small U.S. map inserts showing distributions, and lists of representative collections by state. A total of 197 species were treated, 109 of these in the subgenus *Dichanthelium* Hitchcock & Chase, which was named and described in this treatment.

Hitchcock and Chase made a valiant effort to restrict the recognized species to recognizable taxonomic units. Two hundred and thirty-three previous names were absorbed in synonymy. Forty-seven of the 92 species named by Nash and Ashe were rejected. In the 45 years following the Hitchcock and Chase monograph, many state and regional treatments have been presented. Noteworthy are those of Deam (1929), Weatherby & Griscom (1934), Fernald (1921, 1929, 1934, 1950), Silveus (1942), Shinners (1944), Pohl (1947), Blomquist (1948), and Steyermark (1963). *Dichanthelium* was elevated to generic status by Gould (1974).

Attempts to reduce the number of *Dichanthelium* taxa are seen in the treatments of Radford et al. (1964) in the *Manual of the Vascular Flora of the Carolinas*, and Correll & Johnston (1970) in the *Manual of the Vascular Plants of Texas*. Radford et al. relegated significant numbers of names to synonymy and recognized 40 species in the Carolinas. Correll and Johnston reduced the number of Texas species to 26, from a total of 53 recognized by Hitchcock and Chase. Still further reduction in the number of species in Texas is seen in the treatment of Texas grasses by Gould (1975), who listed only 16.

Selected groups of the dichanthelia have been the subject of one M.S. thesis (J. D. Bacon, 1970), and four Ph.D. dissertations (M. G. Lelong, 1965, R. W. Freckmann, 1967, R. W. Spellenberg, 1968, and C. A. Clark, 1977). Spellenberg (1975) has reported on synthetic hybridization of western North American segregates of *Dichanthelium acuminatum* (as *Dichanthelium lanuginosum*).

The following treatment is based on the study of plant materials collected by the writers throughout the midwestern, eastern, and southcentral portions of the United States and on the specimens of numerous herbaria including MO, NY, TAES, TEX, and US.

In the basic treatment, specific reference to synonyms is restricted to author and date of publication, except for names published after 1962 where a complete citation is given. Except for the few recently proposed names, a relatively complete listing of North American taxa is included in the *Index to Grass Species* (Chase & Niles, 1962), the 1951 revision of Hitchcock's *Manual of the Grasses of the United States*, and the 1910 monograph of *Panicum* by Hitchcock and Chase. Type material examined by the writers is indicated by reference to the herbarium. Species (and variety) distributions are shown in Figs. 1–3. The numbers correspond with the listed numbers of the taxa.

TAXONOMIC RELATIONSHIPS OF *DICHANTHELIUM* AND *PANICUM*[3]

Dichanthelium typically has a growth pattern that distinguishes it from all other North American grasses, including *Panicum*. In all but two species, a basal rosette of short, broad-bladed leaves is produced during autumn and winter, and primary inflorescences are developed on elongated shoots early in the spring. Late spring, summer, and autumn growth in most species produces fascicles of short, branched and rebranched lateral shoots with greatly reduced leaves and lateral inflorescences. *Panicum* species do not normally produce a basal rosette of short, broad leaves nor do they usually have two distinct flowering periods with profuse secondary branching of the culms. *Dichanthelium* begins flowering early in the spring, in February and March in the southern United States, with the species of *Panicum* of the area flowering from a few weeks to as much as five or six months later. All species of *Dichanthelium* are perennial, as are many species of *Panicum*. The type species of *Panicum* (*P. miliaceum* L.), however, is an annual.

Dichanthelium differs from all other North American genera of grasses except *Melica* (Boyle, 1945) in the low incidence of polyploidy. All but three of the United States species are diploid ($2n = 18$), and the exceptional species, *Dichanthelium boscii*, *D. xanthophysum*, and *D. clandestinum*, are tetraploid ($2n = 36$). In contrast, *Panicum* and most other genera of grasses are only 20–30% diploid and 70–80% polyploid.

Brown et al. (1957) determined that the shoot apex of *Panicum* has a single layer of tunica cells, whereas in *Dichanthelium* there is a double layer of cells at the shoot apex. Recent investigations (Brown & Smith, 1972; Smith & Brown, 1973) have shown *Dichanthelium* to differ from *Panicum* and most genera of the subfamily Panicoideae in the intermediate products of photosynthesis. In *Dichanthelium* the initial fixation of carbon is in 3-carbon phosphoglyceric acid, whereas in *Panicum* the initial fixation is in 4-carbon acids (oxaloacetic, malic, aspartic), which, via the Calvin-Benson cycle, are then converted into 3-carbon molecules (Smith & Brown, 1973). The two carbon-fixation pathways are referred to as C_3 and C_4, with the C_4 pathway being associated with high specialization in the structure and function of the vascular bundle sheath cells (in the leaf) and high $^{13}C/^{12}C$ ratios. The C_4 pathway, bundle sheath cell specialization, and high $^{13}C/^{12}C$ ratios are characters of the Kranz syndrome (Smith & Brown, 1973). All *Dichanthelium* species examined for leaf anatomy were C_3 and non-Kranz, while all panicums examined except *P. hians* were C_4 and Kranz. *Panicum hians* Ell., a doubtful *Panicum*, was intermediate. The $^{13}C/^{12}C$ ratios of all species of *Dichanthelium* tested by Brown & Smith (1975) and by the authors were low negative ratios in the range of $-22°/_{oo}$ to $-38°/_{oo}$. Most *Panicum* species reportedly have $\delta^{13}C$ numbers ($^{13}C/^{12}C$ ratios) between -9 and $-18°/_{oo}$ (Smith & Brown, 1973). The data show a gap of about $9°/_{oo}$ (-15 to $-24°/_{oo}$) between the two genera, making them appear completely distinct in respect to carbon-fixation pathways. The assumption that Kranz and

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[3] This discussion is essentially as presented in the Ph.D. dissertation of the second author (Clark, 1977).

non-Kranz conditions are conservative and major contrasting taxonomic characters was mainly responsible for reclassification of subfamilies and tribes of the grass family by Avdulov (1931) and by Stebbins & Crampton (1961). Brown & Smith (1975: 11–12) suggest that:

> . . . the assumption that the Kranz and non-Kranz conditions specify distinctive evolutionary lines of high taxonomic priority, even at the subgeneric level in *Panicum*, could require that the genus be divided on these characters either into two genera or subgenera or into a large number of genera. The type species of *Panicum*, *P. miliaceum* L., is a Kranz species. Therefore, any non-Kranz subgeneric taxa might be removed from the genus into newly-erected genera. Since *Dichanthelium* has long been recognized as having the status of a subgenus based upon distinctive morphological characters and is now known to differ from the type by being a non-Kranz taxon, its elevation to generic status seems justified.

Consistent epidermal differences have been reported in the palea of the upper (perfect) floret of *Dichanthelium* and *Panicum* (Clark & Gould, 1975). The surfaces of *Dichanthelium* palea tips uniformly have simple, rounded papillae, spaced in regular rows, whereas the palea tips of *Panicum miliaceum* and other *Panicum* species studied have irregularly arranged, compound or aggregated papillae. This is a character that has proven to be consistent throughout the Hawaiian and South American species of *Dichanthelium* as well as the North American taxa.

Table 1 presents a comparison of 24 characteristics of *Dichanthelium* and *Panicum*.

Taxonomy

Dichanthelium (Hitchc. & Chase) Gould, Brittonia 26: 59. 1974. Based on *Panicum* L. subgenus *Dichanthelium* Hitchc. & Chase, Contr. U.S. Natl. Herb. 15: 142. 1910. TYPE SPECIES: *Panicum dichotomum* L.

Perennials, typically tufted and usually forming in late summer or early autumn a basal rosette of shorter, broader blades than those of the culms. *Culms* stiffly erect or decumbent-erect, glabrous or hairy, 15–70 cm tall, infrequently to 150 cm or more tall. *Sheaths* of the main culms rounded on the back, often shorter than the culm internodes, glabrous or variously hairy. *Ligule* usually a ring of hairs, infrequently a short membrane or absent. *Culm blades* narrow or broad, usually flat, the reduced blades of secondary branches involute in some species. *Secondary branching* after the first culm growth and elongation often resulting in densely clustered fascicles of often much-reduced leaves and inflorescences. *Inflorescence* typically a small panicle with spreading or occasionally contracted branches, the spikelets short- or long-pediceled. *Spikelets* ovate, elliptical or obovate, awnless, 0.8–4.5 mm long. *Disarticulation* below the glumes. *Glumes* both present, but the lower one often greatly reduced. *First glume* with nerves or nerveless, mostly ¼–⅓ as long as the spikelet but minute in a few species and ¾ the length of the spiklet in others. *Lower floret* usually neuter but staminate in a few species. *Upper floret* perfect, with a shiny, glabrous, coriaceous lemma and palea, the lemma tightly inrolled over the palea. *Palea* apex rounded, with minute, symmetrical papillae in longitudinal rows, and an apical ridge with 7–12 large stomata in one or more rows.

TABLE 1. Comparison of taxonomic characters of *Dichanthelium* and *Panicum*.

Characters	*Dichanthelium*	*Panicum*
Basic Chromosome Number	$x = 9$. All diploid ($2n = 18$) except *D. boscii*, *D. xanthophysum* and *D. clandestinum*, which are tetraploid ($2n = 36$).	$x = 9$, 10. Reported $2n = 18$, 20, 21, 25, 30, 32, 36, 36 + Bs, 40, 42, 44, 45, 48, 49+, 54, and 72 (Carnahan & Hill, 1961).
Chromosome Size	Small and short, uniform.	Small to medium-sized (Brown, 1948).
Apospory	Not reported.	Reported in *P. deustum*, *P. maximum*, *P. obtusum*, and *P. virgatum* (Brown & Emery, 1958).
Embryo Sac Development	Species examined are of the *Polygonum* type.	Usually of the *Polygonum* type, occasionally the *Adoxa* type (Waller, 1976).
Embryo Size	Relatively small in relation to total seed size.	Relatively large in relation to total seed size.
Annuals or Perennials	Perennials only.	Both annuals and perennials, with the type, *P. miliaceum* L., being annual.
Growth Form	Usually a basal rosette of short, broad blades formed in late summer and through winter. Lateral branching often profuse and conspicuous.	Usually no basal rosette of short, broad blades formed. Not sufficient lateral branching to alter overall appearance.
Flowering	Most species begin flowering early in spring and then continue to produce reduced, secondary inflorences until winter frosts.	Most species begin flowering in late spring or summer and usually do not produce reduced, secondary inflorescences.
Inflorescence	An open panicle on terminal shoots and reduced, contracted panicles on branches.	An open or contracted panicle.
General Morphology	Morphologically homogenous.	Morphologically heterogeneous (Brown, 1948).
Spikelet Morphology	Uniform in structure and appearance.	Variable in structure and appearance.
Palea Morphology	Uniform in shape, indurate, with margins inrolled. Paleas of perfect florets with simple, rounded papillae arranged in more or less linear rows at the apex.	Palea morphology variable. Paleas of perfect florets usually with compound or multiple papillae irregularly arranged at the apex (Clark & Gould, 1975).
Ligule	A short, fringed or glabrous membrane, a fringe of hairs, or absent.	A fringed or glabrous membrane, a fringe of hairs, or absent.
Habitat	Moist, humid, most commonly shaded habitats in temperate and subtropical to tropical regions of the Americas; also in bogs and swamps of Hawaii.	Variable habitats, in wet or dry sites, with world-wide distribution in temperate and subtropical to tropical regions.
Culm Anatomy	Cells of assimilatory tissues of random size and arrangement. No layer of well-developed parenchyma separating assimilatory tissue and sclerenchyma fibers.	Assimilatory tissue often of radial chlorenchyma. Usually a layer of well-developed parenchyma separating the assimilatory tissue from the sclerenchyma fibers.

TABLE 1. Continued.

Characters	*Dichanthelium*	*Panicum*
Tunica of Shoot	Shoot apex with 2 layers of tunica cells.	Shoot apex with one layer of tunica cells in species examined (Brown et al., 1957).
Kranz Syndrome Photosynthesis	C_3 photosynthesis (non-Kranz).	C_4 photosynthesis (Brown & Smith, 1972; Smith & Brown, 1973) (Kranz).
Vascular Bundles of Leaf	Outer sheath with no chloroplasts (non-Kranz).	Outer sheath with large, specialized chloroplasts (Kranz).
Chlorenchymatous Cells of Blade Mesophyll	Usually randomly arranged and continuous between vascular bundles, with numerous air spaces (non-Kranz) but occasionally slightly radially arranged. Five or more chlorenchymatous cells intervening between adjacent vascular bundles (non-Kranz).	Often radially arranged around vascular bundles and usually tightly packed and with few air spaces; often interrupted by a region of colorless cells between the vascular bundles. Usually 2–4 chlorenchymatous cells intervening between adjacent vascular bundles (Kranz) (Hattersley & Watson, 1975).
Blades	Only occasionally with pronounced ribs and furrows on both surfaces.	Pronounced ribs and furrows on both surfaces.
Mestome sheath	Always present and continuous around the vascular bundle.	Frequently present, but occasionally absent. When present, often interrupted on one side by fibers.
Stomata	Triangular-shaped or dome-shaped subsidiary cells.	Triangular- or tall, dome-shaped subsidiary cells.
Leaf Epidermis Bicellular micro-hairs	Present, broadest near the mid-portion and tapering towards both ends, with the cells approximately the same length, the distal cell slightly longer.	Present, clavate or tapered, with the distal cell about 1½ times as long as the basal cell.
Silica cells	Cross-, saddle-, or occasionally dumbbell-shaped.	Cross-, saddle-, or dumbbell-shaped.

Key to the Species

1. Basal leaves long, narrow and linear, bright green or bluish-green, mostly 8–20 cm long and seldom more than 5 mm broad (see also *D. aciculare*).
   2. Spikelets (2.9–)3.1–4.5 mm long, with the upper floret shorter than the somewhat beaked second glume and lemma of the lower floret ..... 1. *D. depauperatum*
   2′. Spikelets 2.2–3(–3.2) mm long, the upper floret as long as the beakless second glume and lemma of the lower floret ..... 2. *D. linearifolium*

1′. Basal leaves long or short, not narrow and linear, more than 5 mm broad when as much as 8 cm long.

3. Leaves at base of the plant numerous, relatively long and soft, similar to and only slightly, if at all, shorter than the soft, yellowish green lower culm blades; plants branching only at the base, the slender culms remaining simple; blades mostly 4–10 mm broad.
   4. Sheaths retrorsely pilose; uppermost culm blade 4–7 cm long, at least ¾ as long as those of the basal tuft; blade margins glabrous or finely ciliate .... 3. *D. laxiflorum*
   4′. Sheaths glabrous or ascending-pilose; uppermost culm blade 1.5–6 cm long, less than ¾ as long as the blades of the basal tuft; blade margins coarsely papillose-ciliate ..... 4. *D. leucoblepharis*

3′. Leaves at base of the plant typically forming a basal rosette of short, relatively broad, firm or thin blades, these usually conspicuously shorter than the culm blades; blades 3–25 mm or more broad.
5. Spikelets 3.3–5.2 mm long ..... A
5′. Spikelets 0.8–3.2 mm long ..... AA

A. (Spikelets 3.3–5.2 mm long)

6. Blades of culm leaves, at least some, 13–35 mm broad.
7. First glume usually ¼–⅓ as long as the spikelet; panicle branches and leaf blades spreading.
8. Spikelets broadly elliptic to obovate, turgid, usually with broad, heavy nerves ..... 11. *D. oligosanthes*
8′. Spikelets narrowly elliptic to obovate, not turgid or strongly-nerved.
9. Culm nodes, at least the lowermost, bearded; spikelets 3.8–5.2 mm long.
10. Ligules 1.5 mm or less long; blades glabrous or puberulent; spikelets 4–5.2 mm long ..... 5. *D. boscii*
10′. Ligules 2.5–4 mm long; blades commonly puberulent-tomentose on one or both surfaces but occasionally nearly glabrous; spikelets 3.8–4.2 mm long ..... 14. *D. ravenelii*
9′. Culm nodes glabrous or slightly pubescent; spikelets 3.3–3.8 mm long.
11. Sheaths glabrous or softly villous; blades mostly 8–12(–18) cm long ..... 6. *D. latifolium*
11′. Sheaths, at least the lower ones, papillose-hispid with spreading hairs; blades 10–28 cm long ..... 7. *D. clandestinum*
7′. First glume of at least some spikelets ½ or more as long as the spikelet; panicle branches and leaf blades stiffly erect or only slightly spreading.
12. Blades papillose-hispid on one or both surfaces ..... 12. *D. leibergii*
12′. Blades glabrous on both surfaces ..... 13. *D. xanthophysum*
6′. Blades of culm leaves 12 mm or less broad.
13. Spikelets broadly elliptic or slightly obovate, rounded at the apex; first glume ¼–⅓ as long as the spikelet ..... 11. *D. oligosanthes*
13′. Spikelets narrowly ovate, elliptic, obovate, or obpyriform, rounded or pointed at the apex; first glume short or long.
14. First glume of at least some spikelets commonly ½–⅔ as long as the spikelet; blades of culm leaves typically (7–)8–12 mm broad; spikelets finely pubescent to coarsely hairy; plants of northern and north-central United States and adjacent Canada.
15. Blades papillate-hispid on one or both surfaces; spikelets hairy with usually papillate hairs ..... 12. *D. leibergii*
15′. Blades glabrous on both surfaces, glabrous or ciliate on the margins; spikelets with nonpapillate hairs ..... 13. *D. xanthophysum*
14′. First glume rarely as much as ½ as long as spikelet except in *D. pedicellatum* of Texas; blades of culm leaves 2–7(–9) mm broad; spikelets hairy or glabrous.
16. Spikelets narrowly obpyriform, 3.5–4.3 mm long; first glume appearing distant from the second glume due to the narrow, attenuate base of the second glume; blades characteristically firm, short, and abruptly pointed, usually ciliate on the margins to well above middle; Texas ..... 18. *D. nodatum*
16′. Spikelets narrowly ovate, elliptic, obovate or obpyriform, 3.2–3.9 mm long; first glume not appearing distant from the second glume; blades firm or thin, short or long, usually ciliate on the margins only near the base.
17. Midculm blades firm and stiff, long-acuminate at the apex, seldom over 2.5 mm broad on plants with spikelets 3.3 mm or more long; lower culm internodes glabrous or hairy but not puberulent, spikelets 3.3–3.6 mm long; widespread on Atlantic Coastal Plain and occasional westward ..... 23. *D. aciculare*
17′. Midculm blades thin or firm, 3–8(–12) mm broad, not long acuminate at the apex; lower culm internodes various; spikelets 3.3–3.9 mm long.

18. Lower culm internodes glabrous or hairy but not puberulent; spikelets usually pubescent or short-hispid with papillate hairs, 3.3–3.9 mm long; Texas and northern Mexico .. 19. *D. pedicellatum*
18′. Lower culm internodes minutely puberulent; spikelets 3.3–3.6 mm long, puberulent to glabrous; mainly on Atlantic Coastal Plain, a few records from midwestern United States ..... 20. *D. sabulorum*

AA. (Spikelets 0.8–3.2 mm long)

19. Spikelets 2.1–3.2 mm long ..... B
19′. Spikelets 0.8–2 mm long ..... BB

B. (Spikelets 2.1–3.2 mm long)

20. Blades of primary culms, at least some, 13–25 mm broad C
20′. Blades of primary culms 12 mm or less broad CC

C. (Blades 13–25 mm broad)

21. Culm nodes glabrous or slightly hairy, the internodes typically glabrous; glabrous-glandular band not developed below the culm nodes.
    22. Blades long or short, the lower ones cordate at the base; ligule absent or a ring of hairs; spikelets 2.1–2.9 mm long.
        23. Spikelets (2.1–)2.4–3.2 mm long, narrowly ovate or elliptic.
            24. Sheaths, at least the lower ones, papillose-hispid with stiff, spreading hairs; blades, at least some, 12–20 cm or more long ..... 7. *D. clandestinum*
            24′. Sheaths glabrous or finely pubescent; blades usually less than 10 cm long ..... 8. *D. commutatum*
        23′. Spikelets 2.1–2.2 mm long, broadly elliptic to suborbicular ..... 9. *D. sphaerocarpon*
    22′. Blades, at least some, 12–25 cm long, not cordate at the base; ligule a fringed or glabrous membrane; spikelets 2.2–2.9 mm long ..... 17. *D. scabriusculum*
21′. Culm nodes, at least the lower ones, bearded, the lower internodes with long, spreading hairs; glabrous-glandular band present just below the culm nodes ... 16. *D. scoparium*

CC. (Blades 12 mm or less broad)

25. Blades, at least the lower ones, cordate or subcordate at the base, mostly 6–12 mm broad.
    26. Spikelets narrowly elliptic, 2.1–3.2 mm long.
        27. Larger culm blades broadest near the base, spreading from the culms, usually asymmetrical, when broad then strongly cordate at the base ..... 8. *D. commutatum*
        27′. Larger culm blades broadest at or just below the middle, erect or erect-spreading, narrow below to a moderately cordate-subcordate base ..... 25. *D. boreale*
    26′. Spikelets broadly elliptic or broadly obovoid to subspherical, 2.1–2.2 mm long ..... 9. *D. sphaerocarpon*
25′. Blades not cordate or subcordate at the base, narrow or broad.
    28. Hairs of ligule or pseudoligule, at least some, 2–5 mm long.
        29. Sheaths with hairs 2–4 mm long; nerves of the upper glume and lemma of the lower floret narrow, distinct or indistinct.
            30. Ligule with a dense ring of short hairs in front of a thin line of long hairs ..... 21. *D. ovale*
            30′. Ligule without a dense ring of short hairs in front of the line or ring of long hairs ..... 26. *D. acuminatum*
        29′. Sheaths glabrous, pubescent, or with stiff hairs not over 1.5 mm long; nerves of the upper glume and lemma of the lower floret broad, distinct ..... 11a. *D. oligosanthes* var. *oligosanthes*

28′. Hairs of ligule or pseudoligule less than 2 mm long, or if this long, then culms with a broad, glabrous-glandular band just below the nodes.
31. Culm nodes, at least the lower ones, bearded.
32. Culms tall and stout, with a broad, glabrous-glandular band below the nodes; blades of the lower leaves typically villous or velvety-pubescent ..... 16. *D. scoparium*
32′. Culms tall or short, without a glabrous-glandular band below the nodes.
33. Culm internodes glabrous or the lower ones slightly pilose; culm nodes bearded with long, spreading hairs; blade surfaces glabrous or those of the lower leaves sparsely pilose ..... 24. *D. dichotomum*
33′. Culm internodes, at least the lower ones, strigose or villous; culm nodes bearded with spreading or appressed hairs; blade surfaces glabrous or variously hairy.
34. Culm nodes bearded with long, reflexed or spreading hairs; culm internodes typically with spreading or reflexed, pustulate-based hairs; primary culm blades soft and broad, pilose or villous on both surfaces, 8–12 mm broad ..... 15. *D. malacophyllum*
34′. Culm nodes bearded with erect or less frequently spreading hairs; culm internodes typically with appressed or erect, non-pustulate hairs; primary culm blades firm, mostly 4–8 mm broad.
35. Blades pubescent or strigose on the abaxial surface, glabrous on the adaxial surface or with a few long hairs near the base ..... 21. *D. ovale*
35′. Blades, at least those at the lower nodes, villous or strongly pilose on both surfaces ..... 22. *D. consanguineum*
31′. Culm nodes not bearded, the lowermost nodes sometimes sparsely hairy or puberulent.
36. Plants typically 75–150 cm tall but occasionally much shorter; ligule membranous; first glume less than ⅓ as long as the spikelet, broad and truncate or rounded ..... 17. *D. scabriusculum*
36′. Plants mostly 35–75 cm tall; ligule a ring of hairs or absent; first glume to ⅓ as long as the spikelet.
37. Blades of midculm leaves typically long and stiff, linear or linear-lanceolate and acuminate, when less than 8 cm long then only 2–5 mm broad ..... 23. *D. aciculare*
37′. Blades of midculm leaves lanceolate, thin or firm but not stiff, mostly 3–12 mm broad, when as much as 8 cm long, then usually 7 mm or more broad.
38. Spikelets 2.5–3.2 mm long, broadly elliptic, rounded at the apex; second glume and lemma of the lower floret with broad, rounded nerves ..... 11. *D. oligosanthes*
38′. Spikelets 2.1–3.2 mm long, elliptic or obovate, rounded or pointed at the apex; second glume and lemma of the lower floret with narrow, faint or distinct nerves.
39. Culm internodes and sheaths, at least the lower ones, puberulent or pubescent; plants mostly of the Atlantic Coastal Plain ..... 20. *D. sabulorum*
39′. Culm internodes and sheaths glabrous or sparsely pilose.
40. Culms tending to be stiffly erect; blades erect or erect-spreading, broad, usually but not always, tapering from just below the middle to both ends, often yellowish green; plants not or sparingly branched in age, not developing leafy fascicles of reduced leaves and inflorescences; plants of the northeastern United States and southern Canada ..... 25. *D. boreale*
40′. Culms not stiffly erect; blades usually spreading, broad or narrow, bright green; plants often branching freely in age, becoming top-heavy with a mass of fascicled, reduced leaves and inflorescences;

plants widespread in the eastern, central, and southern United States ..... 24. *D. dichotomum*

BB. (Spikelets 0.8–2 mm long)

41. Hairs of ligule or pseudoligule 2–5 mm long, at least on some ligules.
    42. Ligule with a distinct ring of short hairs in front of the long hairs ..... 21. *D. ovale*
    42′. Ligule without a distinct ring of short hairs in front of the long hairs ..... 26. *D. acuminatum*

41′. Hairs of ligule or pseudoligule absent or short, not over 1.5 mm long.
    43. Lower culm internodes and sheaths puberulent, pubescent, strigose or villous.
        44. Blades of midculm leaves long, narrow, and stiff, acuminate, often becoming involute, mostly 2–5 mm broad even when long ..... 23. *D. aciculare*
        44′. Blades of midculm leaves lanceolate, usually soft, when 8 cm or more long often more than 5 mm broad.
            45. Lower culm internodes cinereous-puberulent to short-pubescent; leaves lacking long hairs except for a fringe on the upper sheath margins and often long cilia on blade margins; lower culm nodes sometimes puberulous but not bearded; spikelets 1.3–2 mm long ..... 20. *D. sabulorum*
            45′. Lower culm internodes variously pubescent, strigose, or villous; leaves with the sheaths usually strigose or villous; the blades often with long hairs on the abaxial surface and occasionally on the adaxial surface; lower culm nodes usually bearded; spikelets 1.5–2 mm long ..... 21. *D. ovale*
    43′. Lower culm internodes, and usually the sheaths, glabrous.
        46. Blades typically thick and glabrous or with a few papillate-hairs on the lower margins.
            47. Blades of the lower culm leaves linear or linear-lanceolate, acuminate, 6 mm or less broad, relatively narrow at the base ..... 23. *D. aciculare*
            47′. Blades of the lower culm leaves lanceolate, mostly 7–30 mm broad; blades broad and subcordate at the base.
                48. Spikelets 1.4–2 mm long.
                    49. Spikelets broadly elliptic or obovoid to subspherical ..... 9. *D. sphaerocarpon*
                    49′. Spikelets narrowly elliptic ..... 8. *D. commutatum*
                48′. Spikelets 1–1.1 mm long ..... 10. *D. erectifolium*
        46′. Blades thin and glabrous or essentially so, broad or narrow, usually not cordate or subcordate but occasionally so in *D. boreale*.
            49. Blades broad, erect or spreading-erect, often yellowish green, tapering from slightly below the middle to both ends, sometimes subcordate at the broad base; plants sparingly branched in age, without fascicled, reduced leafy branches and inflorescences; spikelets 2 mm or more long; plants mostly of northeastern United States and southern Canada ..... 25. *D. boreale*
            49′. Blades broad or narrow, erect or spreading, bright green; plants freely branching in age, becoming top-heavy with a mass of fascicled, reduced leafy branches and inflorescences; spikelets 1.2–2 mm long; plants widespread in eastern and southern United States ..... 24. *D. dichotomum*

1. **D. depauperatum** (Muhl.) Gould, Brittonia 26: 59. 1974. TYPE: ". . . Penns. Carolina."

BASIONYM: *Panicum depauperatum* Muhlenberg, Descr. Gram. 112. 1817.
SYNONYMS: *Panicum strictum* Pursh, 1814, not R. Br., 1810. Fragment and photo of holotype, US.
P. rectum Roemer & Schultes, 1817.
P. involutum Torrey, 1823. Fragment and photo of holotype, US.
P. muhlenbergii Sprengel, 1825.
P. junceum Trinius, 1826.
P. sprengelii Kunth, 1829.

P. depauperatum var. *involutum* Wood, 1861.
P. depauperatum var. *laxum* Vasey, 1889.
P. depauperatum var. *psilophyllum* Fernald, 1921.
P. strictum var. *psilophyllum* (Fernald) Farwell, 1941.

Culms densely tufted, mostly 20–60 cm tall, glabrous or the lowermost nodes and internodes hispid or puberulent. *Plants* in age often becoming bushy-branched and developing small, contracted panicles in the axils of narrow, flat or involute, reduced leaves. *Leaves* pilose or hispid with long hairs to nearly glabrous, the sheaths commonly thinly pilose. *Ligule* a fringe of hairs 0.3–1 mm long. *Blades* linear or some of the lower ones lanceolate, 8–20 cm or more long, 1–5(–6) mm broad, gradually tapering to a long, slender tip, often involute on drying. *Panicles* of the primary culms 4–8(–10) cm long, relatively few-flowered, with short, spreading or erect-spreading branches. *Spikelets* (2.9–)3.1–4.5 mm long, usually glabrous but occasionally sparsely pilose, ovate or elliptic, with the upper floret conspicuously shorter than the narrowly or broadly pointed and somewhat beaked second glume and lemma of the lower floret. *First glume* about ⅓ as long as the spikelet, irregularly lobed, rounded or broadly pointed. *Second glume* strongly 7–9-nerved. *Lemma* of the upper floret broadly rounded and often minutely umbonate at the apex.

HABITAT AND DISTRIBUTION. On open or semiopen grassland sites, often on the disturbed soils of roadsides and ditches. Southeastern Canada (Quebec and Ontario), northeastern and central United States (Newfoundland to Minnesota), south to Georgia and Texas.

2. **D. linearifolium** (Scribner) Gould, Brittonia 26: 60. 1974. TYPE: "Dry soil, especially hillsides, New York and New Jersey to Missouri," *Vasey* in 1882. Holotype, US.

BASIONYM: *Panicum linearifolium* Scribner, in Britton & Brown, Illust. Fl. 3: 500 *fig. 268a.* 1898.
SYNONYMS: *Panicum werneri* Scribner, 1898. Holotype, US.
P. perlongum Nash, 1899. Holotype, NY; isotype, US; fragment and photo of holotype, US.
P. pammeli Ashe, 1900.
P. linearifolium var. *werneri* (Scribner) Fernald, 1921.
P. strictum var. *perlongum* (Nash) Farwell, 1928.
P. strictum var. *linearifolium* Farwell, 1928.
P. strictum var. *linearifolium* subvar. *werneri* (Scribner) Farwell, 1928.
Dichanthelium perlongum (Nash) Freckmann, Phytologia 39: 269. 1978.

Similar to and perhaps intergrading with *D. depauperatum* but the sheaths characteristically densely pilose, the spikelets shorter (2.3–3, occasionally –3.2, mm long), and the upper floret typically rounded or broadly pointed and as long as the second glume and lemma of the lower floret.

HABITAT AND DISTRIBUTION. Frequently present in open woodlands in the eastern part of the range. With the same general range and habitat preference as *D. depauperatum* but present westward to North Dakota, Colorado, and New Mexico.

In 1967, Freckmann recognized only one species, *Panicum depauperatum*, in the *strictum-perlongum-linearifolium* complex and treated *P. perlongum* and

P. linearifolium as varieties. In 1978 he transferred the *perlongum* entity to *Dichanthelium* at the species level (*D. perlongum* [Nash] Freckmann).

3. **D. laxiflorum** (Lamarck) Gould, Brittonia 26: 60. 1974. TYPE: "Amerique Septentrionale." Fragment and photo of holotype in US.

BASIONYM: *Panicum laxiflorum* Lamarck, Encycl. 4: 748. 1798.
SYNONYMS: *Panicum xalapense* H.B.K., 1816.
P. pumilum Bosc ex Nees, 1829, not Lamarck, 1798.
P. rariflorum Ruprecht, 1842, not Lamarck, 1798.
P. ruprechtii Fournier, 1886, not Fenzl, 1854.
P. dichotomum var. *laxiflorum* (Lamarck) Beal, 1896.
P. caricifolium Scribner, 1898.
P. pyriforme Nash, 1899. Isotypes, MO, NY, US.
P. aureum Muhlenberg ex Scribner & Merrill, 1900.
P. xalapense var. *strictirameum* Hitchcock & Chase, 1910.
P. laxiflorum var. *strictirameum* (Hitchcock & Chase) Fernald, 1934.

Plants mostly 15–60 cm tall, with rather long, soft basal blades. *Culms* not branching above the base; *internodes* below the panicle glabrous, the nodes bearded with soft, spreading hairs. *Sheaths* rather uniformly pilose with spreading usually reflexed hairs 2–3 mm long. *Ligule* a glabrous or minutely fringed rim less than 0.5 mm or absent. *Blades* soft, yellowish green mostly 7–16(–20) cm long, 3–10 mm broad, lanceolate or less frequently gradually tapering to an acuminate apex, glabrous or pilose, often ciliate on the margins to well above the middle. *Panicles* open, mostly 4–12 cm long, usually elevated on a long peduncle but occasionally remaining in a basal tuft of leaves; *main panicle axis and branches* usually hirsute with long, soft hairs, the spikelets on short or long pedicels. *Spikelets* pubescent with short spreading hairs, 1.7–2.3 mm long, narrowly ovate or oblong, obtuse or broadly rounded at the apex. *First glume* rounded or broadly pointed at the apex, ca. ⅓ as long as spikelet. *Second glume* and lemma of the lower floret with 7–9 narrow but strong nerves.

HABITAT AND DISTRIBUTION. Usually in shaded, moist habitats. Along the Coastal Plain, Maryland to Georgia and Florida, and westward to Indiana, Missouri, Arkansas, Oklahoma, and Texas; also in Mexico, Guatemala and the Dominican Republic.

The collection *Gould 12521* from near College Station, Brazos County, Texas, appears to be a hybrid. These specimens (at least on the US sheet) have the retrorsely pilose sheaths, and blades with glabrous surfaces and coarsely ciliate margins of *D. laxiflorum*, but have a much-branched habit and relatively short, dark green blades.

4. **D. leucoblepharis** (Trinius) Gould & Clark, comb. nov. TYPE: Hitchcock & Chase (1910) state "A specimen in the Trinius Herbarium is labeled: 'ab. Enslino in Am. bor. 1. dt. cl. Trattinick.' This is typical *P. ciliatum* Ell. . . . the Enslin specimen has been chosen as the type."

BASIONYM: *Panicum leucoblepharis* Trinius, Clav. Agrost. 234. 1822. *Panicum ciliatum* Elliott, 1816, not Maercklin, 1792.

Plants densely tufted, with the leaves mostly in a basal tuft. *Culms* 5–35 cm

tall, not branching above the base and thus not developing fascicles of reduced floriferous secondary branches above the base. *Sheaths* glabrous or pilose, most frequently hairy on the margins. *Ligule* a minute fringe of hairs, much less than 1 mm long. *Blades* typically short and broad, mostly 3–6 cm long and 3–8 mm broad, usually coarsely ciliate with stiff, papilla-based hairs to well above the middle, the *uppermost leaf blade* usually much shorter than those below. *Panicles* open, few-flowered, mostly 3–5 cm long, scarcely elevated above the basal tuft of leaves or well-exserted on long peduncles; *panicle axis* usually pilose with spreading hairs. *Spikelets* 1.1–2.1 mm long, glabrous to pubescent or puberulent, elliptic or slightly obovate, broadly pointed or rounded at the apex. *First glume* broadly pointed or rounded at apex, ⅓–½ as long as the spikelet. *Second glume* and lemma of the lower floret usually 7-nerved, the nerves weakly or strongly developed.

Key to the varieties

a. Spikelets puberulent or pubescent, 1.5–2.1 mm long; blade surfaces glabrous ..... 4A. *D. leucoblepharis* var. *leucoblepharis*

aa. Spikelets glabrous, 1.1–1.8 mm long.

b. Blade surfaces glabrous; spikelets 1.2–1.8 mm long ..... 4B. *D. leucoblepharis* var. *glabrescens*

bb. Blade surfaces pilose or hispid; spikelets 1.1–1.5 mm long ..... 4C. *D. leucoblepharis* var. *pubescens*

4A. **D. leucoblepharis** (Trinius) Gould & Clark. var. **leucoblepharis**.

SYNONYMS: *Panicum ciliatum* Elliott, 1816, not *P. ciliatum* Maercklin, 1792.
P. ciliatifolium Kunth, 1829.
P. ciliatifolium Desvaux, 1831.

As Veldkamp (1976) has recently noted, the name *Panicum ciliatum* Elliott (Bot. S.C. and Ga. 1: 126. 1816) cannot be considered the basionym for this species as the combination *Panicum ciliatum* was first published by F. Maercklin (Schrift. Regensb. Bot. Ges. 1: 332–334. Regensburg) as a species *Digitaria*.

HABITAT AND DISTRIBUTION. In shaded to somewhat open areas of pine forest, mostly in sandy, acidic soils. Along the Coastal Plain from North Carolina to Florida, Mississippi, and Texas.

4B. **D. leucoblepharis** (Trinius) Gould & Clark var. **glabrescens** (Grisebach) Gould & Clark, comb. nov. TYPE: Jamaica, *Purdie*. Holotype, K, examined by Hitchcock.

BASIONYM: *Panicum dichotomum* L. var. *glabrescens* Grisebach, Fl. Brit. W. Indies 553. 1864.
SYNONYM: *Panicum polycaulon* Nash, 1897. Holotype, NY; fragment and photo of holotype, US.

Culms slender, 15–45 cm tall; blades of culm leaves short, to 6 mm broad, coarsely ciliate on the margins.

HABITAT AND DISTRIBUTION. Usually in open woodlands in low, sandy, acidic soil. Southern Georgia, Alabama, Mississippi, Louisiana, and Florida, also in the Antilles.

4C. **D. leucoblepharis** (Trinius) Gould & Clark var. **pubescens** (Vasey) Gould & Clark, comb. nov. TYPE: *Curtiss*, North American Plants No. H. Lectotype, US, selected by Hitchcock.

BASIONYM: *Panicum laxiflorum* Lam. var. *pubescens* Vasey, Contr. U.S. Natl. Herb. 3: 30. 1892.
SYNONYMS: *Panicum strigosum* Muhlenberg, 1816. Holotype, NY; fragment and photo of holotype, US.
P. longipedunculatum Scribner, 1894.

Autumnal plants forming dense mats with the inflorescences not or only slightly overtopping the leaves.

HABITAT AND DISTRIBUTION. In the United States, along the Coastal Plain from southeastern Virginia to Florida and Texas, and also reported from Tennessee; also in eastern Mexico, the Antilles, Central America, and northern South America.

5. **D. boscii** (Poiret) Gould & Clark, comb. nov. TYPE: "Recueillie a Caroline par *M. Bosc.*" Fragment and photo of lectotype, US.

BASIONYM: *Panicum boscii* Poiret in Lamarck, Encycl. Suppl. 4: 278. 1816.
SYNONYMS: *Panicum waltheri* Poiret, 1816, not Pursh, 1814.
P. latifolium L. var. *australe* Vasey, 1889.
P. latifolium var. *molle* (Vasey) Hitchcock & Chase, 1889. Holotype, US.
P. waltheri var. *molle* (Vasey) Porter, 1893.
P. porterianum Nash, 1895.
P. pubifolium Nash, 1899. Syntypes, NY.
P. boscii var. *molle* (Vasey) Hitchcock & Chase, 1908.

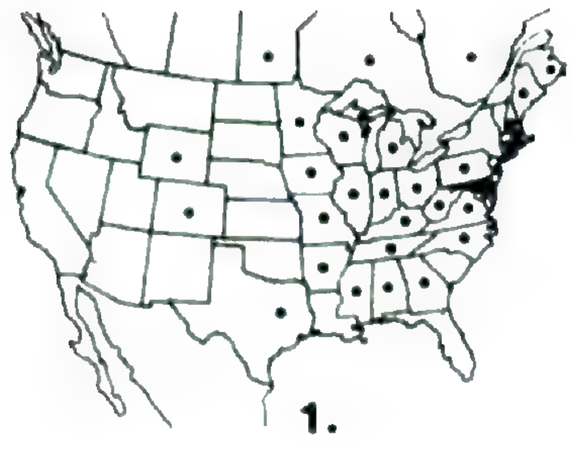
Culms stout, few to several in small clumps, 40–70 cm tall, in age branching above and often becoming "top-heavy" and reclining; the internodes glabrous, puberulent or papillose, the nodes retrorsely bearded. *Sheaths* glabrous, puberulent, or papillose-pilose. *Ligule* a fringe of hairs ca. 1 mm long. *Blades* glabrous to pubescent or villous on one or both surfaces, 7–12 cm long, 15–30 mm broad, often asymmetrical, sparsely ciliate at the usually broadly cordate base. *Panicles* 4–10 cm long, to 8 cm broad, with stiffly erect-spreading, usually puberulent branches. *Spikelets* papillose-pubescent, narrowly ellipsoid to obovate, (3.7–) 4–5.2 mm long. *First glume* ⅓–⅔ the length of the spikelet. *Lower floret* often staminate.

HABITAT AND DISTRIBUTION. Usually in shaded, well-drained forest sites. Connecticut and Massachusetts to northern Florida and westward to Illinois, Missouri, Oklahoma, and eastern Texas.

6. **D. latifolium** (L.) Gould & Clark, comb. nov. TYPE: "Habitat in America." Fragment and photo of holotype, US.

BASIONYM: *Panicum latifolium* L., Sp. Pl. 58. 1753.
SYNONYMS: *Milium latifolium* (L.) Moench, 1794.
Panicum macrocarpon LeConte ex Torrey, 1818. Holotype, NY; fragment and photo of holotype, US.
P. schnecki Ashe, 1900.

Culms 45–80(–100) cm tall, glabrous or sparsely pubescent, the lower nodes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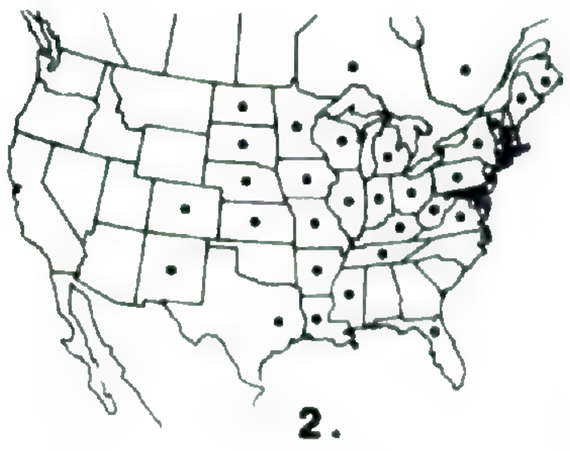
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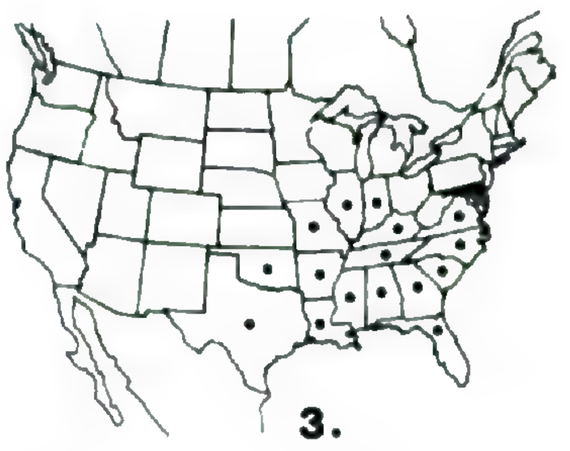
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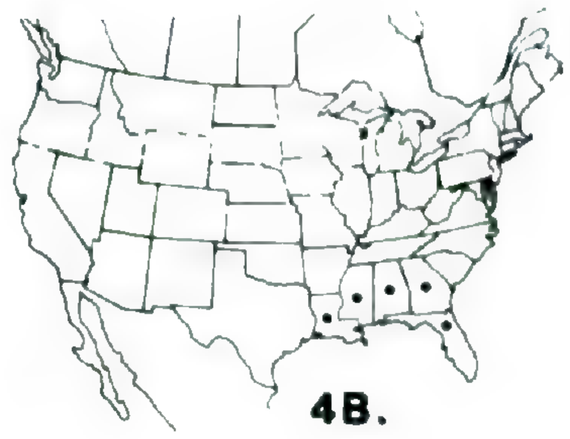
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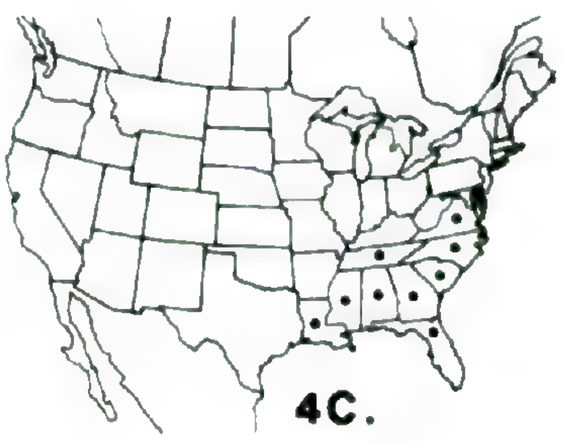
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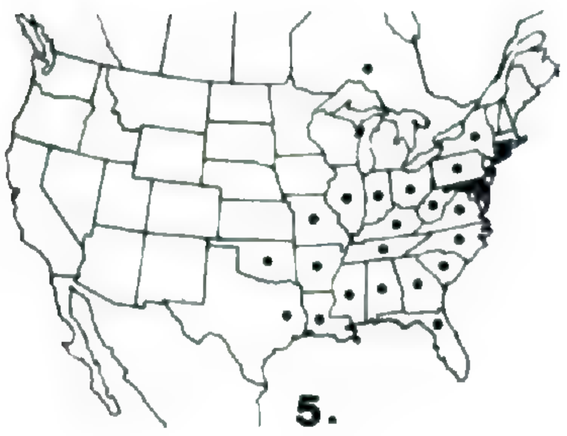
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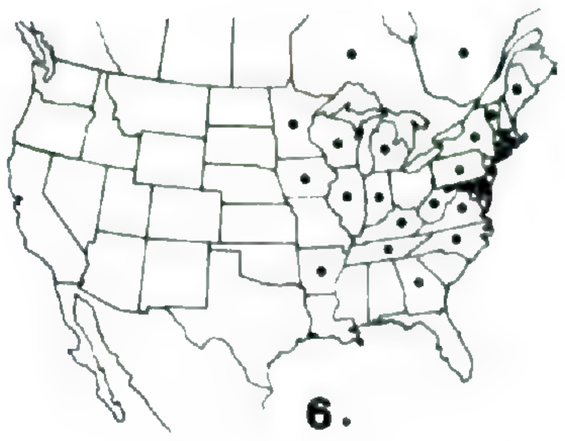
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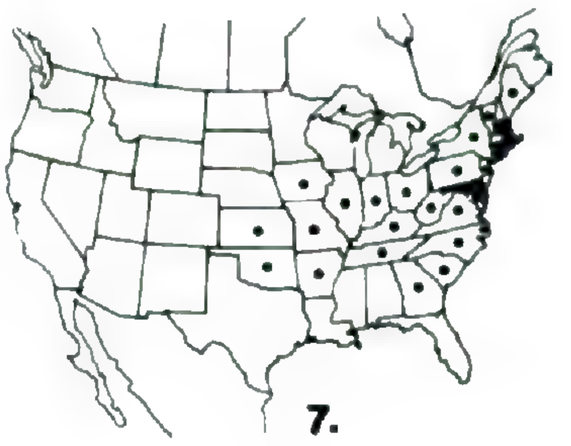
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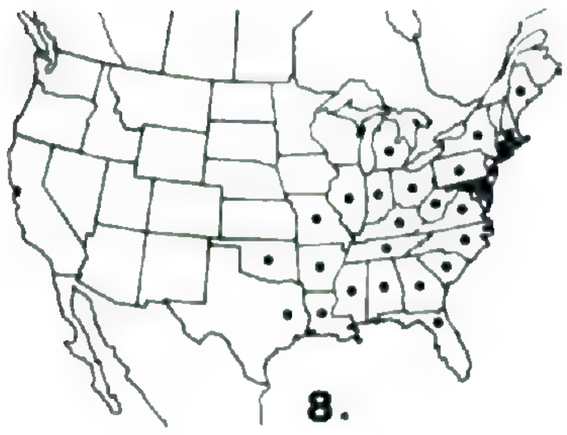
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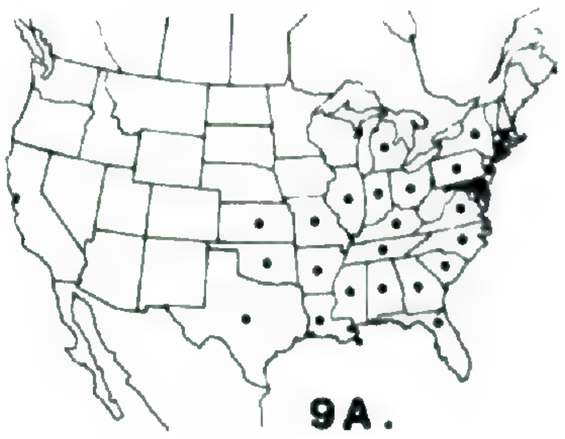
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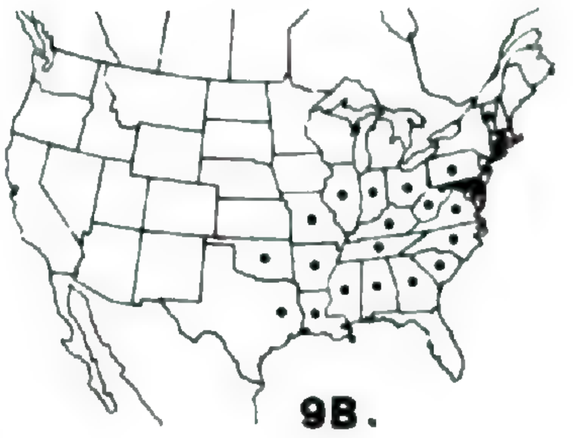
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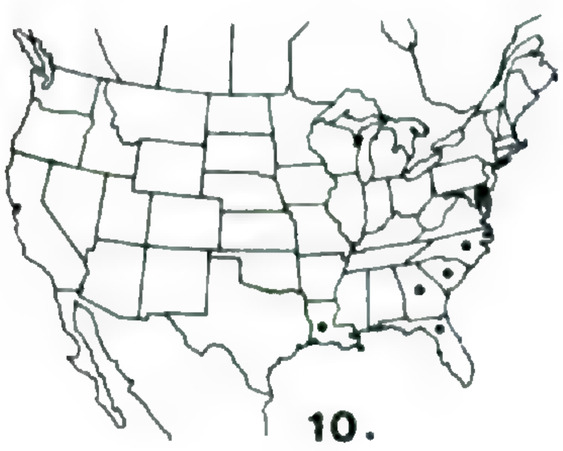
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11A.

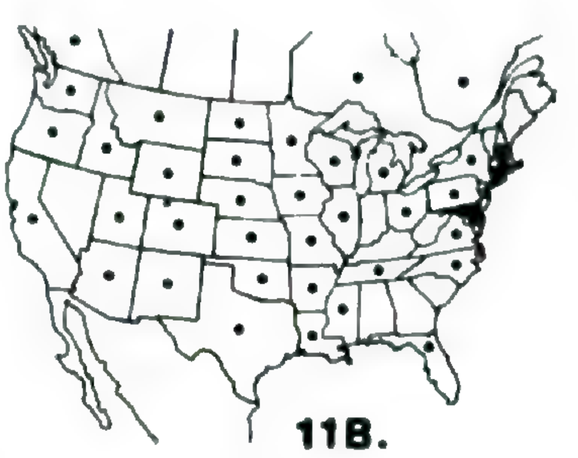

11B.

FIGURE 1. *D. depauperatum*. 2. *D. linearifolium*. 3. *D. laxiflorum*. 4A. *D. leucoblepharis* var. *leucoblepharis*. 4B. *D. leucoblepharis* var. *glabrescens*. 4C. *D. leucoblepharis* var. *pubescens*. 5. *D. boscii*. 6. *D. latifolium*. 7. *D. clandestinum*. 8. *D. commutatum*. 9A. *D. sphaerocarpum* var. *sphaerocarpon*. 9B. *D. sphaerocarpon* var. *isophyllum*. 10. *D. erectifolium*. 11A. *D. oligosanthes* var. *oligosanthes*. 11B. *D. oligosanthes* var. *scribnerianum*.

and sheath bases occasionally inconspicuously hairy. *Sheaths* shorter than the internodes, frequently ciliate with soft hairs on the margins, glabrous or sparsely pilose on the back, usually soft-hairy on the collar. *Ligule* a minute fringed membrane, rarely as much as 1 mm long. *Blades* thin, glabrous on both surfaces,

broadly cordate at the base, mostly 8–12(–18) cm long and 13–35 mm broad, usually not or only slightly asymmetrical. *Panicles* with spreading or erect-spreading branches, 6–15(–20) cm long, relatively few-flowered, the branches glabrous or scabrous. *Spikelets* narrowly ellipsoid, broadly pointed, puberulent to nearly glabrous, 3.3–3.8 mm long. *First glume* ⅓–½ as long as the spikelet.

HABITAT AND DISTRIBUTION. In well-drained, shady forest sites. Maine to northern Georgia and westward to Wisconsin, Illinois, Tennessee, and Mississippi.

Dichanthelium latifolium appears closely related to *D. clandestinum* and to *D. commutatum.*

7. **D. clandestinum** (L.) Gould, Brittonia 26: 59. 1974. TYPE: "Habitat in Jamaica, Pennsylvania, *Kalm.*" The reference to Jamaica by Linnaeus must be in error.

BASIONYM: *Panicum clandestinum* L., Sp. Pl. 58. 1753.
SYNONYMS: *Milium clandestinum* (L.) Moench, 1794.
Panicum latifolium var. *clandestinum* (L.) Pursh, 1814.
P. pedunculatum Torrey, 1823. Fragment and photo of holotype, US.
P. clandestinum L. var. *pedunculatum* (Torrey) Torrey, 1841.
P. decoloratum Nash, 1899. Holotype, NY; isotype, US.
Chasea clandestina (L.) Nieuwland, 1911.

Culms rather stout, 40–80(–125) cm tall, often from stout rhizomes 5–10 cm long, usually in large clumps; *internodes* glabrous to scabrous or papillose-hispid, the nodes glabrous or slightly hairy. *Sheaths*, at least the lower ones, papillose-hispid with stiff hairs, usually with soft hairs on the collar. *Ligule* a minute, fringed membrane, never over 1 mm long. *Blades* glabrous or scabrous, 10–20 (–28) cm long and mostly 12–30 cm broad, cordate at the base. *Panicles* usually open, 8–15 cm long and 6–9 cm broad, with spreading or erect-spreading branches; *axis and branches* glabrous or scabrous. *Spikelets* narrowly ovate to elliptic, puberulent, more or less pointed at the apex, (2.3–)2.7–3.5(–4) mm long. *First glume* usually ⅓–⅔ as long as the spikelet.

HABITAT AND DISTRIBUTION. In moist, often sandy soil of shaded or slightly open sites in and along woodlands, often in ditches and low areas. Southeastern Canada and the eastern half of the United States from Maine to northern Florida and westward to Iowa, Kansas, and Texas.

The stiff, coarse hairs of the sheath are often bristly and reportedly irritating to the skin. *Dichanthelium clandestinum* appears closely related to *D. latifolium*, differing mainly in the bristly sheaths and the usually longer leaf blades.

8. **D. commutatum** (Schultes) Gould, Brittonia 26: 59. 1974. TYPE: No specimen or definite locality indicated.

BASIONYM: *Panicum commutatum* Schultes, Mant. 2: 242. 1824.
SYNONYMS: *Panicum nervosum* Muhlenberg ex Elliott, 1816, not Lamarck, 1797.
P. umbrosum LeConte ex Torrey, 1818, not Retzius, 1786. Lectotype, NY; fragment and photo of lectotype, US.
P. enslini Trinius, 1826. Fragment and photo of holotype and isotype, US.
P. polyneuron Steudel, 1854.

P. leiophyllum Fournier, 1886, not Nees, 1829.
P. joorii Vasey, 1889. Holotype, US; isotype, MO.
P. commutatum var. *minus* Vasey, 1889.
P. commutatum var. *latifolium* Scribner, 1893.
P. manatense Nash, 1897. Fragment and photo of holotype, US.
P. commelinaefolium Ashe, 1898. Holotype, NY.
P. ashei Pearson ex Ashe, 1898. Isolectotype, MO, NY, US.
P. equilaterale Scribner, 1898. Lectotype, US; isolectotype, US.
P. currani Ashe, 1899.
P. epilifolium Nash, 1899. Holotype, NY; fragment and photo of holotype, US.
P. subsimplex Ashe, 1900. Isotypes, MO, NY.
P. mutabile Scribner & Smith ex Nash, 1903. Holotype, NY; isotype, US.
P. commutatum var. *ashei* (Pearson ex Ashe) Fernald, 1934.

Culms tufted, usually slender and wiry, 15–75 cm tall, usually glabrous but the lower nodes and internodes occasionally pubescent but not puberulent. *Sheaths* usually shorter than the internodes, ciliate on the margins, glabrous or less frequently puberulent on the back, often pubescent on the sides of the collar and occasionally across the collar. *Ligule* absent or a fringe of hairs less than 1 mm long. *Blades* exceedingly variable in size, moderately thick or firm, the lower ones broadest below the middle, typically asymmetrical and strongly to moderately cordate at the base, mostly 4–9(–12) cm long and 8–25 mm broad, usually glabrous on the surfaces and papillate-ciliate on the lower margins. *Panicles* open, those of the main culm 5–10(–14) cm long about ½ as broad as long, with spreading or spreading-erect branches. *Spikelets* on short or rather long pedicels, narrowly elliptic, glabrous or puberulent (2–)2.4–3.2 mm long. *First glume* ⅓–½ as long as the spikelet, rounded or broadly pointed. *Lemma* of the upper floret often minutely apiculate.

HABITAT AND DISTRIBUTION. Mostly in low shaded, moist sites in and along woodlands. Throughout the eastern coastal states, Maine, and Massachusetts to Florida, and westward to Michigan, Missouri, Oklahoma, and Texas; also in Mexico.

9. **D. sphaerocarpon** (Elliott) Gould, Brittonia 26: 60. 1974. TYPE: Georgia.

BASIONYM: *Panicum sphaerocarpon* Elliott, Bot. S.C. & Ga. 1: 125. 1816.

Plants developing a winter rosette of conspicuous, broad, short, thick basal blades, these often with a narrow white border. *Culms* 20–80 cm tall, in age branching at the middle and upper nodes to produce fascicles of reduced leaves and inflorescences, the leaf blades short and flat, the nodes glabrous or appressed-pubescent. *Ligule* absent or a fringe of hairs to 1 mm long. *Culm blades* broad, moderately thick, glabrous on the surfaces, ciliate with papillate hairs on the lower margins, cordate-clasping at the base. *Panicles* open, 5–15(–18) cm long, with spreading lower branches to 8 cm long; axis and branches glabrous. *Spikelets* puberulent to glabrous, broadly elliptic or broadly obovoid to subspherical, 1.4–2.2 mm long. *First glume* acute or broadly rounded at the apex, mostly ⅕–¼ as long as the spikelet.

Key to the varieties

a. Mid-culm blades 6–11(–14) mm broad, the uppermost blade usually 3–9 cm long ..... 9A. *D. sphaerocarpon* var. *sphaerocarpon*

aa. Mid-culm blades, at least some, 15–30 mm broad, the uppermost blade usually 10–15 cm or more long ..... 9B. *D. sphaerocarpon* var. *isophyllum*

9A. **D. sphaerocarpon** (Elliott) Gould var. **sphaerocarpon**.

SYNONYMS: *Panicum kalmii* Swartz ex Wikstrom, 1829.
P. heterophyllum Swartz ex Wikstrom, 1829, not Sprengel, 1822, nor Bosc ex Nees, 1829.
P. dichotomum L. var. *sphaerocarpon* (Elliott) Wood, 1861.
P. nitidum Lamarck var. *crassifolium* A. Gray, 1877.
P. microcarpon Muhlenberg var. *sphaerocarpon* (Elliott) Vasey, 1883.
P. vicarium Fournier, 1886.
P. inflatum Scribner & Smith, 1899. Holotype, US; isotype, MO.
P. mississippiense Ashe, 1900.
P. sphaerocarpon var. *inflatum* (Scribner & Smith) Hitchcock & Chase, 1910.

HABITAT AND DISTRIBUTION. Throughout eastern United States, west to Michigan, Kansas, Oklahoma, and Texas, and south through Mexico, in woodlands, brushy areas, and old fields.

Plants with ligules 0.3–1 mm long and leaf blades with more or less parallel margins were recognized by Hitchcock & Chase (1910) as *P. sphaerocarpon* var. *inflatum*. *Wolff 3964* from Milam Co., Texas, has a ligule of dense hairs ca. 3 mm long and hispid-pubescent sheaths. This could be a *D. sphaerocarpon–D. acuminatum* hybrid.

9B. **D. sphaerocarpon** (Elliott) Gould var. **isophyllum** (Scribner) Gould & Clark, comb. nov. TYPE: Tennessee, Blount Co., Alleghany Springs, *E. E. Gayle*, August 1890.

BASIONYM: *Panicum microcarpon* Muhlenberg var. *isophyllum* Scribner, Bull. Agric. Exp. Sta. Univ. Tennessee 7: 51. *fig.* 54. 1894. *Panicum microcarpon* Muhlenberg (1817) is a later homonym of *P. microcarpon* Muhlenberg ex Elliott, 1816. The name *isophyllum* Scribner is the earliest varietal name to be applied to this taxon and must be retained even though the species basionym, *microcarpon*, is illegitimate.
SYNONYMS: *Panicum multiflorum* Elliott, 1816, not Poiret, 1816. Fragment and photo of holotype, US.
P. microcarpon Muhlenberg, 1817, not Muhlenberg ex Elliott, 1816. Fragment and photo of holotype, US.
P. polyanthes Schultes, 1824.
P. firmandum Steudel, 1855.
Dichanthelium sphaerocarpon var. *polyanthes* (Schultes) Gould, Brittonia 26: 60. 1974.

HABITAT AND DISTRIBUTION. Mostly in well-drained shaded, woodland areas. Vermont to Georgia and westward to southern Illinois, Missouri, Oklahoma, and eastern Texas.

In *D. sphaerocarpon* var. *isophyllum* the upper culm leaves are conspicuously enlarged and sometimes the uppermost culm leaf is the largest, measuring as much as 25 cm long and 3 cm broad. The inflorescences of var. *isophyllum* tend to be larger than those of var. *sphaerocarpon*, occasionally reaching 18 cm or more in length and 8 cm in width.

10. **D. erectifolium** (Nash) Gould & Clark, comb. nov. TYPE: "Florida."

BASIONYM: *Panicum erectifolium* Nash, Bull. Torrey Bot. Club 23: 148. 1896. Based on *P. sphaerocarpon* Elliott var. *floridanum* Vasey, 1889. Isotype, MO.
SYNONYM: *Panicum floridanum* Chapman, 1897, not Trinius, 1834.

Plants rather stout, 30–70 cm tall, with culms stiffly erect, in small to large clumps. *Culms* typically 4–7-noded. *Herbage* essentially glabrous, the blade margins usually ciliate. *Sheaths* shorter than the internodes. *Blades* of culm leaves firm, erect or erect-spreading, short, usually 4–8 cm long but occasionally longer, 6–9(–14) mm broad. *Panicles* 5–10 cm long, characteristically loosely contracted and densely flowered with very small spikelets; *axis and branches* glabrous. *Spikelets* broadly elliptic to suborbicular, puberulent to nearly glabrous, 1–1.2 mm long. *First glume* mostly ¼ or less as long as the spikelet.

HABITAT AND DISTRIBUTION. Mostly in moist or wet soil of marshy, low pine forest. Along the Coastal Plain, North Carolina to Florida and westward to Louisiana.

This species is rather common in the low, moist pine barrens of Florida and occasional at other southeastern localities in moist habitats. Its affinities obviously are with *Dichanthelium sphaerocarpon*.

11. **D. oligosanthes** (Schultes) Gould, Brittonia 26: 60. 1974. TYPE: Georgia.

BASIONYM: *Panicum oligosanthes* Schultes, Mant. 2: 256. 1824. Based on *Panicum pauciflorum* Elliott, 1816, not R. Brown, 1810.

Culms loosely to densely tufted, rather wiry, 15–85 cm long, branching in age to produce fascicles of reduced leaves and small, secondary panicles. *Sheaths* glabrous to densely papillate-hispid, the margins usually ciliate. *Ligule* a dense fringe of hairs 0.1–4.2 mm long. *Primary culm blades* firm, 3–14 cm long, 3–12(–15) mm broad, broad at the base but not cordate. *Panicles* 4–13 cm long, broad or narrow. *Secondary panicles* 2–5 cm long, little if at all exserted, usually with only 1–9 spikelets. *Spikelets* glabrous to pilose or papillose-pilose, broadly elliptic or ovate, blunt or broadly pointed at the apex, 2.5–4 mm long, 1.2–2.2 mm broad. *First glume* broadly pointed, mostly ¼–⅓ as long as the spikelet.

Key to the varieties

a. Ligule usually 1.6 mm or more long; abaxial leaf surface usually tomentose, occasionally puberulent ..... 11A. *D. oligosanthes* var. *oligosanthes*
aa. Ligule usually less than 1.6 mm long; abaxial leaf surface puberulent or hirsute to glabrous, never tomentose.
  b. Culms mostly 25–60 cm tall, in small or large clumps; blades of the lower culm leaves mostly 7 mm or more broad, glabrous or puberulent, spreading or somewhat erect spreading; primary panicles usually well exserted on long peduncles, about as broad as long; spikelets mostly 3–4 mm long ..... 11B. *D. oligosanthes* var. *scribnerianum*
  bb. Culms mostly 10–25 cm tall, densely tufted; blades 3–6 mm broad, very firm, erect or erect-spreading, long-hirsute on both surfaces; panicles only slightly, if at all, exserted above the leaves; spikelets 2.7–3.4 mm long ..... 11C. *D. oligosanthes* var. *wilcoxianum*

11A. **D. oligosanthes** (Schultes) Gould var. **oligosanthes**.

SYNONYMS: *Panicum pauciflorum* Elliott, 1816. Fragment and photo of holotype, US.
P. scoparium Lamarck var. *angustifolium* Vasey, 1889. Lectotype, US.
P. scoparium var. *pauciflorum* Scribner, 1894.

Culms usually puberulent to villous. *Blades* narrowly acuminate, mostly 5–8

mm broad, broad at the base but not cordate. *Lowermost internode of panicle* axis usually villous or tomentose. *Spikelets* mostly 3.3–4 mm long.

HABITAT AND DISTRIBUTION. Eastern United States from Massachusetts to Florida and west to Minnesota, Nebraska, and Texas; no records seen from New York, Pennsylvania, W. Virginia, Kentucky and Tennessee but probably also present in these states.

11B. **D. oligosanthes** (Schultes) Gould var. **scribnerianum** (Nash) Gould, Brittonia 26: 60. 1974. TYPE: Massachusetts, near Deerfield, *Cooley*. Fragment of holotype, US; isotype, MO.

BASIONYM: *Panicum scribnerianum* Nash, Bull. Torrey Bot. Club 22: 421. 1895. Based on *Panicum macrocarpon* Torrey, 1823, not LeConte, 1819.
SYNONYMS: *Panicum scoparium* S. Watson ex Nash, 1895, not Lamarck, 1798.
P. helleri Nash, 1899. Holotype, NY; isotype, US.
P. pernervosum Nash, 1899. Holotype, NY; fragment and photo of holotype, US; isotype, MO.
P. oligosanthes var. *scribnerianum* (Nash) Fernald, 1934.
P. oligosanthes var. *helleri* (Nash) Fernald, 1934.

Blades glabrous to puberulous. *Lowermost internodes of panicle axis* glabrous, scabrous or puberulous. *Spikelets* mostly 2.7–3.3 mm long but varying from 2.5–4 mm, glabrous to pilose or papillate-pilose.

HABITAT AND DISTRIBUTION. Usually growing in exposed loamy or loamy-clay sites, often in brushy areas. Ontario to British Columbia and throughout the United States but infrequent in the southeastern and western states; also present in northern Mexico.

Relatively glabrous plants with small spikelets were referred by Hitchcock & Chase (1910) and Hitchcock (1935, 1951), to *Panicum helleri* Nash.

11C. **D. oligosanthes** var. **wilcoxianum** (Vasey) Gould & Clark, comb. et stat. nov. TYPE: Nebraska, Fort Niobrara, *Wilcox* in 1888. Holotype, US; isotype, NY.

BASIONYM: *Panicum wilcoxianum* Vasey, U.S.D.A. Div. Bot. Bull. 8: 32. 1889.
SYNONYMS: *Milium wilcoxianum* (Vasey) Lunell, 1915.
Dichanthelium wilcoxianum (Vasey) Freckmann, Phytologia 39: 269. 1978.

Plants short and relatively stout; culms rarely over 25 cm tall, in small or large clumps or tufts. *Culms*, *sheaths* and *blades* papillose-hirsute. *Blades* firm, usually stiffly erect, mostly 5–8 cm long and 3–6 mm broad. *Panicles* small, few-flowered, mostly 2–5 cm long. *Spikelets* mostly 2.5–3.4 mm long.

HABITAT AND DISTRIBUTION. On open, well-drained, grassland sites. Manitoba, Saskatchewan, Alberta, Minnesota and North Dakota, south to Illinois, Kansas, Colorado, and New Mexico.

12. **D. leibergii** (Vasey) Freckmann, Phytologia 39: 271. 1978. TYPE: Iowa, Plymouth Co., *J. Leiberg 34*. Holotype, US.

BASIONYM: *Panicum scoparium* Lamarck var. *leibergii* Vasey, U.S.D.A. Div. Bot. Bull. 8: 32. 1889.

SYNONYMS: *Panicum scribnerianum* Nash var. *leibergii* (Vasey) Scribner, 1897.
P. leibergii (Vasey) Scribner, 1898.
Milium leibergii (Vasey) Lunell, 1915.
Panicum leibergii var. *baldwinii* Lepage, 1959. Isotype, US.

Culms 25–75 cm tall, usually puberulent or pubescent at least on the lower internodes. *Sheaths* papillose-hispid with spreading hairs. *Ligule* a minute fringed or glabrous membrane not over 0.5 mm long including the hairs. *Blades* papillose-hispid on one or both surfaces, papillose-ciliate on the margins, mostly 6–15 cm long and (6–)7–15 mm broad, tending to be erect on the culm, the uppermost blade usually short and reduced. *Panicles* narrow or open, mostly 6–15 cm long. *Spikelets* oblong-obovate, papillose-hispid with spreading hairs, (3.1–)3.3–4 mm long. *First glume* variable in development, often ½ and occasionally ¾ as long as the spikelet.

HABITAT AND DISTRIBUTION. In open woodlands and well-drained prairies. Ontario, Manitoba, and Saskatchewan, to Pennsylvania, Michigan, and North Dakota, and south to southern Ohio, Indiana, Missouri, and Kansas.

The collection *Bush 419*, from McDonald Co., Missouri, probably is a hybrid.

13. **D. xanthophysum** (A. Gray) Freckmann, Phytologia 39: 271. 1978. TYPE: New York, Oneida Co., near Oneida Lake. Lectotype, US; isolectotypes, MO, US.

BASIONYM: *Panicum xanthophysum* A. Gray, N. Amer. Gram. & Cyp. 1: no. 28. 1834. Fragment of lectotype, US; isolectotype, US.
SYNONYMS: *Panicum xanthophysum* f. *amplifolium* Scribner, 1900. Holotype, US.

Culms 25–60 cm tall, glabrous or the lower internodes minutely puberulent. *Sheaths* papillose-pilose and ciliate at least near the apex, often nearly glabrous. *Blades* thin, glabrous except for the ciliate margins, mostly 8–15 cm long and (6–)8–20 mm broad, the uppermost culm blade not or only slightly reduced in size, sometimes longer than those below. *Panicles* 5–12 cm long, typically narrow, contracted and few-flowered, the stiff branches erect or nearly so. *Spikelets* broad or narrow, usually elliptic-obovate, (3.2–)3.5–4 mm long, pubescent. *First glume* variable in development, ⅓–⅔ as long as the second glume and lower lemma.

HABITAT AND DISTRIBUTION. In well-drained prairies. Quebec to Ontario, south to Pennsylvania, Michigan, Wisconsin, Minnesota, and Iowa.

14. **D. ravenelii** (Scribner & Merrill) Gould, Brittonia 26: 60. 1974. TYPE: South Carolina. Fragment and photo of holotype, US.

BASIONYM: *Panicum ravenelii* Scribner & Merrill, U.S.D.A. Div. Agrost. Bull. 24: 36. 1901. Fragment and photo of holotype, US.
SYNONYM: *Panicum scoparium* Lamarck var. *majus* Vasey, 1889. Holotype, US.

Culms rather stout, to 75 cm tall, the internodes glabrous or pubescent with erect or spreading hairs, the nodes retrorsely bearded; when internodes hairy, then culms often with a broad glabrous band below the bearded nodal area. *Sheaths* coarsely hairy, the hairs often long and papillate. *Ligule* a fringe of

hairs usually 2.5–4 mm long. *Blades* 8–15 cm long, 10–25 mm broad, typically puberulent-tomentose on the abaxial surface and glabrous on the adaxial surface but occasionally glabrous or puberulent on both surfaces. *Panicles* open, few-flowered, mostly 9–12 cm long, the panicle axis usually hairy, with either or both short and long hairs. *Spikelets* pubescent, broadly oblong to obovate, rounded at the apex, 3.7–5 mm long. *First glume* ca. ⅓ or slightly more as long as the spikelet.

HABITAT AND DISTRIBUTION. In sandy woodlands. Delaware and Virginia south to Florida and west to Iowa, Missouri, eastern Oklahoma, and eastern Texas.

15. **D. malacophyllum** (Nash) Gould, Brittonia 26: 60. 1974. TYPE: Oklahoma, "Indian Territory," Sapulpa, 1895, *Bush 1228*. Holotype, NY; isotypes, MO.

BASIONYM: *Panicum malacophyllum* Nash, Bull. Torrey Bot. Club 24: 198. 1897. Fragment and photo of holotype, US; isotypes, MO.
SYNONYM: *Panicum scoparium* Lamarck var. *minus* Scribner, 1894. Lectotype, US.

Culms 30–70 cm tall, the internodes pilose or papillose-pilose with spreading hairs, at least below, the nodes retrorsely bearded. *Plants* in age developing dense fascicles of short branches and short, flat leaves. *Herbage* pubescent to villous throughout, often with long and short hairs intermingled, the blades velvety-pilose on both surfaces. *Sheaths* loose, shorter than the internodes, usually less strongly pilose than the culms. *Ligules* 1–1.5 mm long. *Blades* mostly 6–10 cm long, 5–12 mm broad, narrowing to the base, ciliate on the lower margins. *Panicles* 3–7 cm long, usually densely pubescent, the branches first erect and then spreading, the lower main branches often with short, spikelet-bearing branches in their axils. *Spikelets* elliptic, papillate-pilose, mostly 2.9–3 mm long. *First glume* about ⅓ as long as the spikelet.

HABITAT AND DISTRIBUTION. In sandy woodlands. Missouri and Kansas south to Tennessee, Arkansas, Oklahoma, and Texas.

16. **D. scoparium** (Lamarck) Gould, Brittonia 26: 60. 1974. TYPE: "Caroline," *Michaux*. Fragment and photo of holotype, US.

BASIONYM: *Panicum scoparium* Lamarck, Encycl. 4: 744. 1798. Fragment and photo of holotype, US.
SYNONYMS: *Panicum pubescens* Lamarck, 1798.
P. viscidum Elliott, 1816. Fragment and photo of holotype, US.
P. pauciflorum Michaux, 1825.
P. nitidum Lamarck var. *velutinum* Doell, 1877.
P. scoparium Lamarck var. *genuinum* Scribner, 1894.
P. laxiflorum var. *pubescens* (Lamarck) Chapman, 1897.
Chasea pubescens (Lamarck) Nieuwland, 1911.

Culms coarse and thick, to 150 cm tall, in age usually becoming much-branched and developing dense fascicles of reduced leaves and inflorescences. *Lower culm internodes*, *sheaths*, and *blades* velvety-pubescent or velvety-pilose, the upper culms and leaves often moderately pubescent to essentially glabrous.

Culms with a broad, glabrous, glandular-blotched band or zone just below the nodes. *Ligule* a dense ring of hairs 1–2 mm long. *Blades* of main culm mostly 10–25 cm long and 10–20 mm broad, the blades of the fascicled branches short, broad and flat. *Primary panicles* large and open at maturity, mostly 10–18 cm long and 8–14 cm broad. *Spikelets* finely pubescent or occasionally glabrous, ovate or oblong, 2.2–2.8 mm long, rounded or broadly pointed at the apex. *First glume* small, poorly developed, often vestigial.

HABITAT AND DISTRIBUTION. In sandy soils of woodlands and low moist ditches and swales. Massachusetts and New Jersey south along the Coastal Plain to Florida and west to Michigan, Missouri, Oklahoma, and Texas; also in Mexico and the Antilles.

Dichanthelium scoparium most frequently grows in open or partially open ditches and presents a coarse, weedy aspect. When growing in association with other dichantheliums it tends to flower later than all other species.

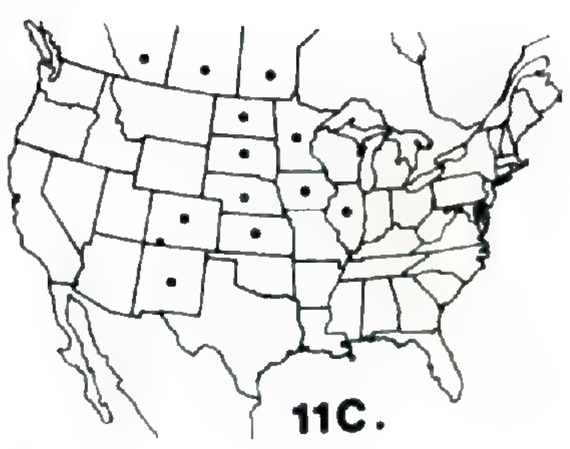
17. **D. scabriusculum** (Elliott) Gould & Clark, comb. nov. TYPE: Georgia, *Baldwin*. Fragment and photo of holotype, US.

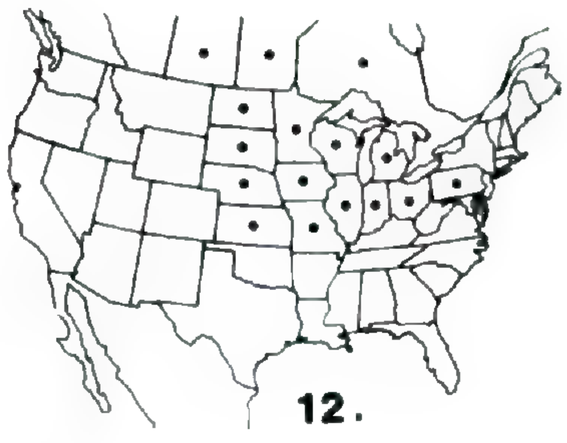
BASIONYM: *Panicum scabriusculum* Elliott, Bot. S.C. & Ga. 1: 121. 1816.
SYNONYMS: *Panicum lanuginosum* Bosc ex Sprengel, 1825, not Elliott, 1816.
P. eriophorum Schultes, 1827.
P. nealleyi Vasey, 1886. Holotype, US.
P. dichotomum L. var. *elatum* Vasey, 1889. Lectotype, US.
P. viscidum Elliott var. *scabriusculum* (Elliott) Beal, 1896.
P. cryptanthum Ashe, 1900.
P. aculeatum Hitchcock & Chase, 1906. Holotype, US; isotype, NY.
P. recognitum Fernald, 1938. Holotype, US; isotype, US.

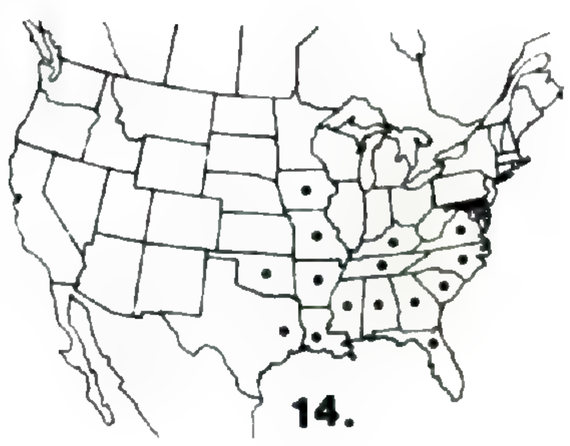
Culms mostly 90–150 cm tall, glabrous, hispid or the internodes puberulent below, often with a light-colored or mottled band or zone of glandular tissue below each node, in age becoming much-branched and developing fascicles of reduced leaves and inflorescences. *Sheaths* shorter than the internodes, glabrous or hispid, often mottled or white-spotted. *Ligule* a minute membrane, usually with a ring of short hairs immediately above. *Blades* elongate, mostly 15–25 cm long and 9–13(–15) mm broad, with parallel margins for most of the length, often more or less pubescent on the abaxial surface but otherwise glabrous or scabrous. *Primary panicles* open, 10–18(–20) cm long, as much as 15 cm broad. *Spikelets* broadly ovate, abruptly narrowing to a point, 2.2–2.9 mm long. *First glume* variable, often greatly reduced or vestigial, occasionally as much as ⅓ as long as the spikelet.

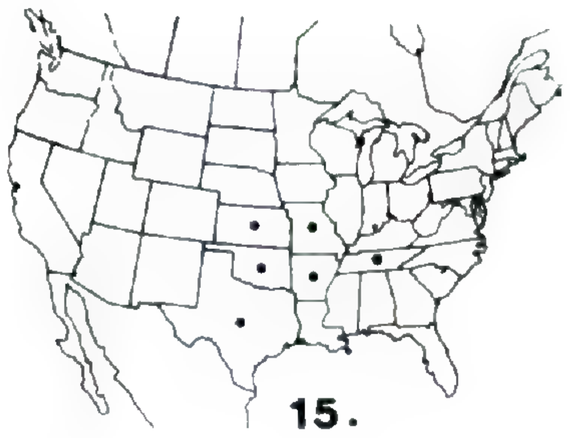
HABITAT AND DISTRIBUTION. Moist, low, usually shaded sites, often along ditches, streams, and swales. On the Coastal Plain, New York, New Jersey and Maryland to Georgia and Florida, and westward to Arkansas, Louisiana, and eastern Texas.

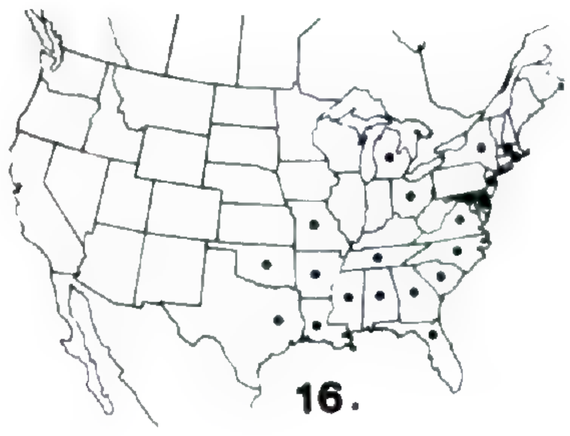
18. **D. nodatum** (Hitchcock & Chase) Gould, Brittonia 26: 60. 1974. TYPE: Texas, Kenedy Co., Sarita, *Hitchcock 3865*. Holotype US; isotypes MO, US.

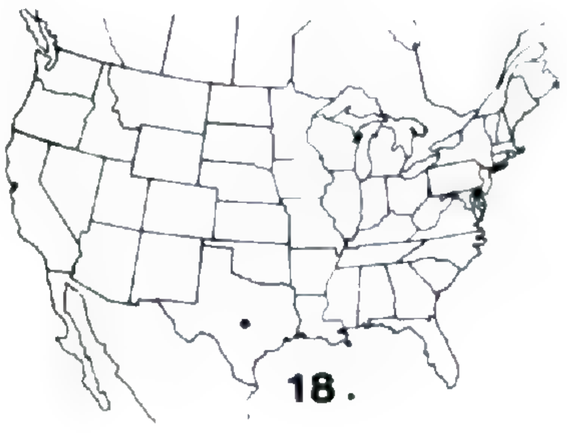


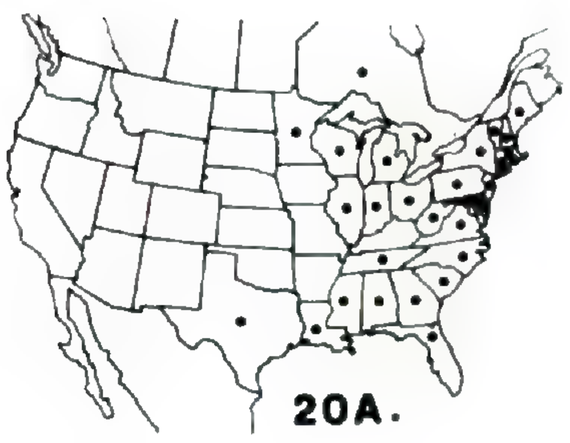


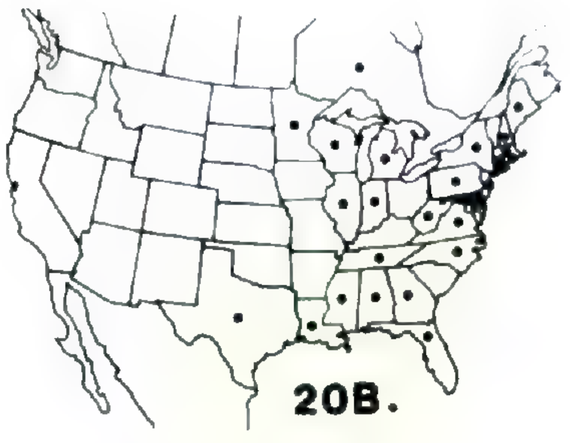












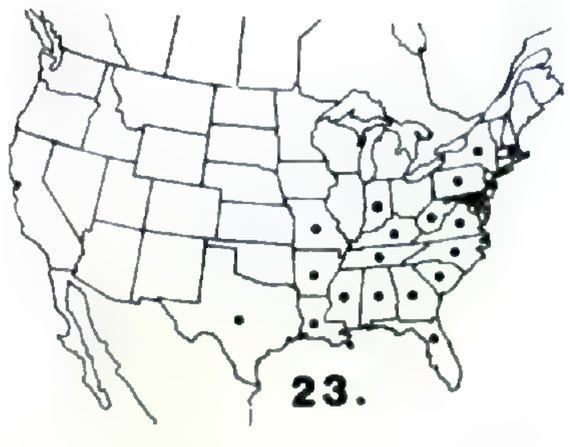


FIGURE 2. 11C. *P. oligosanthes* var. *wilcoxianum*. 12. *D. leibergii*. 13. *D. xanthophysum*. 14. *D. ravenelli*. 15. *D. malacophyllum*. 16. *D. scoparium*. 17. *D. scabriusculum*. 18. *D. nodatum*. 19. *D. pedicellatum*. 20A. *D. sabulorum* var. *patulum*. 20B. *D. sabulorum* var. *thinium*. 21A. *D. ovale* var. *ovale*. 21B. *D. ovale* var. *addisonii*. 22. *D. consanguineum*. 23. *D. aciculare*.

BASIONYM: *Panicum nodatum* Hitchcock & Chase, Contr. U.S. Natl. Herb. 15: 293. 1910.

Culms 20–50(–65) cm tall, subrhizomatous at the base, and often with numerous nodes and short internodes, the internodes scabrous or puberulent to short-hispid, the lower nodes usually inconspicuously hairy. *Sheaths*, at least

the lower ones, short-pubescent with spreading hairs. *Ligule* a dense tuft of hairs 1–2 mm long. *Blades* typically thick, firm, short and broad, minutely puberulent on both surfaces, usually 3–9 cm long, 4–7(–9) mm broad, usually papillose-ciliate on the margins to well above the middle. *Panicles* few-flowered, 4–9 cm long, most frequently narrow and with ascending branches and appressed branchlets. *Spikelets* puberulent, narrowly obpyriform, tapering from above the middle to the base, 3.5–4.3 mm long. *First glume* acute, mostly about ⅓ as long as the spikelet but usually some glumes longer, appearing distant from the second glume due to the narrow, attenuate base of the second glume. *Lemma* of upper floret often minutely puberulent at the tip.

HABITAT AND DISTRIBUTION. Open woods, oak motts, and brushy coastal grasslands, usually in sandy soils. Sandy grasslands and oak motts of southern Texas, Robertson, Bastrop, Edwards counties south to the southern tip of the state and northern Mexico.

19. **D. pedicellatum** (Vasey) Gould, Brittonia 26: 60. 1974. TYPE: Texas, Kimble Co., *Reverchon 1620*. Holotype, US; isotypes, NY, TAES.

BASIONYM: *Panicum pedicellatum* Vasey, U.S.D.A. Div. Bot. Bull. 8: 28. 1889.

Culms 20–70 cm tall from a knotty base, puberulent or hirsute, at least below. *Sheaths* glabrous, pubescent, or papillate-strigose. *Ligule* a minute, fringed membrane or a ring of hairs 0.3–1 mm long, occasionally with a few longer hairs. *Blades* flat, glabrous or sparsely appressed pilose or puberulent, usually ciliate with a few long papilla-based hairs near the base, 4–12 cm long, 3–7(–8) mm broad, narrow at the base and acuminate at the apex. *Panicles* narrow or open, 3–10 cm long, with erect or spreading branches and appressed branchlets and pedicels. *Pedicels* of lateral spikelets usually shorter than the spikelets. *Spikelets* narrowly obovate, 3.3–3.9 mm long, usually pubescent or short-hispid with papillate hairs but occasionally glabrous. *First glume* acute, commonly about ½ length of the spikelet.

HABITAT AND DISTRIBUTION. Usually growing in limey soil on well-drained, partially shaded or open rocky sites. Edwards Plateau of Texas, Bosque, to Bexar, Uvalde, and Val Verde counties; also in northeastern Mexico.

20. **D. sabulorum** (Lamarck) Gould & Clark, comb. nov. TYPE: Uruguay, Montevideo, *Commerson*.

BASIONYM: *Panicum sabulorum* Lamarck, Encycl. 4: 744. 1798.

Culms erect or trailing at the base, often much-branched, 15–60 cm tall, usually with numerous nodes and short internodes, at least the lowermost minutely puberulent to short-pubescent, rarely glabrous. *Leaves* typically glabrous on the surfaces and glabrous or pubescent on the upper sheath margins, often coarsely ciliate on the blade margins at and occasionally above the base. *Ligule* a ring of hairs 0.2–1(–1.5) mm long. *Blades* thin, lanceolate, glabrous or puberulent, never with long hairs except for the marginal cilia, mostly 3–9 cm long and 3–8(–12) mm broad. *Panicles* 3–9 cm long, typically open in age and

occasionally with reflexed branches. *Spikelets* puberulent to glabrous, 1.8–3.6 mm long, elliptic or slightly obovate, broadly rounded at the apex. *First glume* broad or narrow, pointed, usually ⅓ or less as long as the spikelet.

Key to the varieties

a. Spikelets 1.8–3.6 mm long; primary panicles often more than 6 cm long; midculm blades often 7 cm or more long ..... 20A. *D. sabulorum* var. *patulum*
aa. Spikelets 1.3–1.7 mm long; primary panicles mostly 2.5–4 cm long; midculm blades 2–5(–6) cm long ..... 20B. *D. sabulorum* var. *thinium*

20A. **D. sabulorum** (Lamarck) Gould & Clark var. **patulum** (Scribner & Merrill) Gould & Clark, comb. nov. TYPE: Florida, Mantee Co., Braidenton, *Combs 1296*. Holotype, US.

BASIONYM: *Panicum nashianum* Scribner var. *patulum* Scribner & Merrill, U.S.D.A. Dept. Agrost. Circ. 27: 9. 1900.
SYNONYMS: *Panicum lancearium* Trinius, 1826. Fragment of holotype, US.
P. webberianum Nash, 1896. Holotype, NY; isotypes, MO, NY.
P. nashianum Scribner, 1897. Isotype, MO.
P. tsugetorum Nash, 1898. Holotype, NY; fragment and photo of holotype, US.
P. patentifolium Nash, 1899. Holotype, NY; isotypes, MO, NY, US.
P. onslowense Ashe, 1900. Isotype, US.
P. lanuginosum var. *siccanum* Hitchcock & Chase, 1906. Holotype, US.
P. patulum (Scribner & Merrill) Hitchcock, 1906.
P. lancearium var. *patulum* (Scribner & Merrill) Fernald, 1934.
P. euchlamydeum Shinners, 1944.
P. commonsianum Ashe var. *euchlamydeum* (Shinner) Pohl, 1947.

Blades tending to be aggregated towards the base of the plant, the upper blades often much-reduced; in plants referred to *Panicum webberianum* Nash, the lower blades rather thick, broad (8–12 mm) and abruptly acute, usually with a few long cilia at the base. *Spikelets* 1.8–3.6 mm long, usually puberulent but occasionally glabrous.

HABITAT AND DISTRIBUTION. Growing mostly in moist sand of low woodland borders. On the Coastal Plain, Massachusetts to Georgia, Florida, Mississippi, and Louisiana, a few scattered records from Michigan, Wisconsin, and Tennessee. One record from northeastern Mexico.

20B. **D. sabulorum** (Lamarck) Gould & Clark var. **thinium** (Hitchcock & Chase) Gould & Clark, comb. nov. TYPE: New Jersey, Tom's River, *A. Chase 3577*. Holotype, US.

BASIONYM: *Panicum unciphyllum* Trinius var. *thinium* Hitchcock & Chase, Rhodora 8: 209. 1906. Holotype, US.
SYNONYMS: *Panicum portoricense* Desvaux ex Hamilton, 1825.
P. heterophyllum Bosc ex Nees, 1829, not Sprengel, 1822.
P. columbianum Scribner, 1897. Isotype, NY.
P. psammophilum Nash, 1899. Holotype, NY; isotype, US.
P. pauciciliatum Ashe, 1900. Lectotype and isolectotype, US; photo of lectotype, US.
P. oricola Hitchcock & Chase, 1906. Isotypes, MO, NY.
P. columbianum var. *thinium* Hitchcock & Chase, 1908.
P. heterophyllum var. *thinium* (Hitchcock & Chase) Hubbard, 1912.
P. columbianum var. *oricola* (Hitchcock & Chase) Fernald, 1934.
Dichanthelium columbianum (Scribner) Freckmann, Phytologia 39: 270. 1978.

Culms 15–50 cm tall, usually crisp-puberulent below but occasionally short-

pilose, much-branched in age and with fascicled floriferous secondary branches, these with short, flat (not aciculate) blades. *Sheaths*, at least the lower ones, puberulent or short-pilose. *Ligules* a thin or dense ring of hairs 0.2–1(–1.5) mm long. *Blades* of culm leaves lax or firm, lanceolate, most commonly glabrous on the adaxial surface and puberulent on the abaxial surface but occasionally glabrous or puberulent on both surfaces, mostly 2.5–5(–6) cm long and 3–6 mm broad, usually ciliate on the margins. *Panicles* mostly 2.5–4 cm long. *Spikelets* 1.3–1.7 mm long, usually puberulent. *First glume* rarely more than ⅓ as long as the spikelet.

HABITAT AND DISTRIBUTION. In low, moist woodlands and cutover forestland. Coastal Plain, Maine to Florida, Louisiana, and also in scattered localities in New York, Michigan, Wisconsin, Indiana, Illinois, and Texas.

Plants of both var. *patulum* and var. *thinium* of *D. sabulorum* occasionally have slightly longer hairs than typical on the culms and sheaths. These probably represent an intermediate stage or transition to *D. ovale* which typically has strigose or villous sheaths and bearded culm nodes. There also seems to be an associated trend towards narrower and firmer blades leading to *D. aciculare*, possibly through *D. ovale* at least in part.

21. **D. ovale** (Elliott) Gould & Clark, comb. nov. TYPE: Georgia, St. Mary's, *Baldwin*. Fragment and photo of holotype, US.

BASIONYM: *Panicum ovale* Elliott, Bot. S.C. & Ga. 1: 123. 1816.

Plants tufted, leafy at the base. *Culms* 20–50 cm tall, the lower nodes and internodes strigose, less commonly villous or pilose, the upper nodes often glabrous or nearly so, the culms frequently branched and rebranched at the upper nodes, the branchlets with short, flat blades but the branches rarely appearing congested or fasciated. *Lower sheaths* strigose or pilose on the back with long hairs or intermixed long and short hairs, the upper sheaths sparsely pilose. *Ligule* a dense ring of hairs 0.5–1.5 mm long, often with a thin line of hairs (pseudoligule) 2–3 mm long immediately above. *Blades* of culm leaves firm, ascending, often ciliate on the lower margins, lanceolate to lanceolate-acuminate, 6–10 cm long, 5–10 mm broad, acuminate at the apex, the adaxial surface glabrous or sparsely hispid with long, stiff hairs, the abaxial surface glabrous or pubescent with short hairs. *Panicles* open, 5–9 mm long and nearly as broad as long. *Spikelets* pubescent to nearly glabrous, narrowly oblong-elliptic. *First glume* ⅓ to nearly ½ as long as the second glume and lemma of the lower floret.

Many populations of *D. ovale* closely approach the highly variable *D. acuminatum* in morphological characteristics. In the southern portion of the range of *D. ovale*, the presence of a double ring of hairs in the ligular area sometimes is difficult to determine and the separation of both varieties of *D. ovale* from *D. acuminatum* var. *villosum* is not always satisfactory.

Key to the varieties

a. Spikelets 2.6–3.1 mm long ..... 21A. *D. ovale* var. *ovale*
aa. Spikelets 1.5–2.5 mm long ..... 21B. *D. ovale* var. *addisonii*

21A. **D. ovale** (Elliott) Gould & Clark var. **ovale**.

SYNONYMS: *Panicum ciliferum* Nash, 1897. Holotype NY; isotypes, MO, US; fragment and photo of holotype, US.
P. malacon Nash, 1897. Holotype, NY; isotypes, MO, NY, US.
P. strictifolium Nash, 1899. Holotype, NY; isotypes, NY, US.
P. erythrocarpon Ashe, 1900.

HABITAT AND DISTRIBUTION. In sandy, well-drained forestland and along woods borders. New York and New Jersey to Michigan and Wisconsin, and south to Florida, and eastern Texas. Rather infrequent over most of its range but common throughout Florida.

21B. **D. ovale** (Elliott) Gould & Clark var. **addisonii** (Nash) Gould & Clark, comb. nov. TYPE: New Jersey, Wildwood, *Bicknell* in 1897. Holotype, NY.

BASIONYM: *Panicum addisonii* Nash, 1898. Holotype, NY; fragment and photo of holotype, US.
SYNONYMS: *Panicum commonsianum* Ashe, 1898. Isotype, NY.
P. wilmingtonense Ashe, 1900.
P. alabamense Ashe, 1900, not Trinius, 1854. Isotypes, NY, US.
P. owenae Bicknell, 1908. Holotype, NY; isotypes, NY, US.
P. commonsianum subsp. *addisonii* (Nash) Stone, 1911.
P. commonsianum var. *addisonii* (Nash) Fernald, 1935.
P. mundum Fernald, 1936. Isotypes, MO, NY, US.
P. commonsianum var. *addisonii* (Nash) Pohl, 1947.
P. columbianus Scribn. var. *commonsianum* (Ashe) McNeill & Dore, Naturaliste Canad. 103: 562. 1976.
Dichanthelium commonsianum (Ashe) Freckmann, Phytologia 39: 271. 1978.

Culms tending to be much-branched with short, narrow, rather stiff, lanceolate or acuminate blades. *Culms and sheaths* strigose-pubescent, occasionally with a few short hairs intermixed. *Blades* of culm leaves usually glabrous on both surfaces, infrequently with a few soft hairs or a few long stiff hairs. *Spikelets* pubescent, elliptic or obovate, broadly rounded at the apex, 1.5–2.5 mm long.

HABITAT AND DISTRIBUTION. Most frequent on the Atlantic Coastal Plain, Connecticut and New York to Georgia and northern Florida but occasional at widely scattered localities throughout the eastern and midwestern states, ranging westward to Minnesota, Iowa, Oklahoma, and Texas and northern Mexico.

22. **D. consanguineum** (Kunth) Gould & Clark, comb. nov. TYPE: Florida, no specific locality indicated.

BASIONYM: *Panicum consanguineum* Kunth, Rév. Gram. 1: 36. 1829. Based on *P. villosum* Elliott, Bot. S.C. & Ga. 1: 124. 1816.
SYNONYMS: *Panicum villosum* Elliott, not Lamarck, 1791. Fragment and photo of holotype, US.
P. commutatum Schultes var. *consanguineum* (Kunth) Beal, 1896.
P. georgianum Ashe, 1898. Holotype, US.
P. deamii Hitchcock & Chase, 1929. Holotype, US.

Culms 20–60 cm tall, with bearded nodes and densely ascending-villous internodes. *Sheaths* villous. *Ligules* absent or short, not over 1 mm long. *Blades of midculm leaves* 7–11 cm long, 5–8 mm broad, villous on both surfaces, usually

involute at the narrow apex, tapering slightly to the base. *Blades of secondary branches* short, flat and narrow. *Panicles* 4–8 cm long, often contracted and appearing "compact." *Spikelets* puberulent, 2.5–2.8 mm long, narrowly elliptic-obovate, rounded at the apex. *First glume* about ⅓ as long as the spikelet.

HABITAT AND DISTRIBUTION. In dry or moist sandy soils of open or cut-over woodlands. Occasional, Virginia, North Carolina, Indiana, Tennessee, Georgia, Florida, Louisiana, and Texas.

This species appears closely related to the two varieties of *D. ovale* and all have bearded nodes and appressed-strigose or appressed-villous internodes and sheaths.

23. **D. aciculare** (Desvaux ex Poiret) Gould & Clark, comb. nov. TYPE: "Habitat in india orientale." Holotype in P (not seen); fragment and photo of holotype, US. Hitchcock & Chase (1910) stated that the type collection "is without doubt from the southeastern United States."

BASIONYM: *Panicum aciculare* Desvaux ex Poiret in Lamarck, Encycl. Suppl. 4: 274. (July) 1816. Fragment and photo of holotype, US.
SYNONYMS: *Panicum angustifolium* Elliott, (Dec.) 1816. Holotype, US.
P. setaceum Muhlenberg, 1817.
P. subuniflorum Bosc ex Sprengel, 1825.
P. nitidum Lamarck var. *angustifolium* (Elliott) A. Gray, 1835.
P. redivivum Trinius ex Steudel, 1841.
P. curtisii Steudel, 1854.
P. neuranthum Grisebach, 1866. Holotype, NY.
P. neuranthum Grisebach var. *ramosum* Grisebach, 1866. Isotypes, MO, NY.
P. nemopanthum Ashe, 1898. Isolectotype, US.
P. arenicolum Ashe, 1898. Lectotype, US; isolectotypes, NY.
P. ovinum Scribner & Smith, 1899. Holotype, US.
P. delawarense Ashe, 1900. Isotype, US.
P. pungens Muhlenberg ex Scribner & Merrill, 1900, not Poiret, 1816.
P. filirameum Ashe, 1900. Isotype, US.
P. arenicoloides Ashe, 1900. Fragment and photo of holotype, US.
P. orthophyllum Ashe, 1900. Fragment and photo of isotype (?), US.
Panicum fusiforme Hitchcock, 1909.
Chasea angustifolia (Elliott) Nieuwland, 1911.
P. bennettense W. V. Brown, 1942.
P. pinetorum Swallen, 1942. Holotype, US.
Dichanthelium angustifolium (Elliott) Gould, Brittonia 26: 59. 1974.

Plants with a basal rosette of thick, broad, short blades. *Culms* usually stiffly erect, 25–75 cm tall, glabrous or moderately pubescent or pilose but the nodes not truly bearded, in age often branching freely above, producing fascicles of reduced leaves and panicles, the leaves narrow, often involute. *Sheaths* glabrous, pubescent or pilose, occasionally with long, papillate hairs. *Ligule* usually a fringe of hairs 1 mm or less long. *Blades of midculm leaves* firm or stiff, narrowly lanceolate, usually acuminate, glabrous or hairy, mostly 6–15(–20) cm long and 2–6(–8) mm broad, sometimes becoming tightly involute. *Panicles* open or tightly contracted, mostly 4–9 cm long. *Spikelets* elliptic-ovate to obpyriform or fusiform, glabrous or puberulent, 1.9–3.6 mm long. *First glume* usually ¼–⅓ (–½) as long as the spikelet.

HABITAT AND DISTRIBUTION. Frequent on dry sandy soil of open woods and

cut-over forestlands. Atlantic Coastal Plain from Massachusetts and New York to Florida and central Texas, occasional eastward to Indiana, Missouri, and Arkansas; also south through the Antilles, Mexico and Central America to northern South America.

A statistical analysis of morphological variation patterns in populations herein referred to *D. consanguineum*, *D. ovale*, *D. sabulorum*, and *D. aciculare* (Allred & Gould, 1978) shows that within geographic regions these taxa comprise rather well defined groups. When variation patterns from several regions are superimposed, however, the boundaries between groups break down and a continuum of attribute variation is approached. The recognition of only four species and six varieties in this complex to which almost 50 species names have been applied admittedly is somewhat arbitrary and certainly not entirely satisfactory. This treatment, however, is believed to be the best disposition of the populations involved on the basis of available data.

24. **D. dichotomum** (L.) Gould, Brittonia 26: 59. 1974. TYPE: "Habitat in Virginia," *Clayton 458*. Fragment and photo of holotype, US.

BASIONYM: *Panicum dichotomum* L., Sp. Pl. 58. 1753.

Culms slender, 15–80(–100) cm tall, becoming much-branched and "bushy" in age (autumnal phase), the internodes glabrous (the lowermost rarely puberulent), the nodes glabrous or bearded with long spreading hairs. *Sheaths* glabrous on the back, ciliate or pubescent with soft hairs on the margins. *Ligules* absent or a ring of short hairs not over 1 mm long. *Panicles* mostly 2–8(–10) cm long, the late-formed, lateral panicles much-reduced and few-flowered; *axis and branches* glabrous. *Spikelets* oblong or obovate, puberulent or glabrous, 1.2–2.9 mm long, those of the primary panicles usually on long pedicels.

Key to the varieties

a. Blades of the lower culm leaves short or long, usually more than 4 mm broad when as much as 7 cm long.
  b. Ligules 1–1.8 mm long; spikelets 1.3–1.5 mm long; sheaths and lower blades, at least some, sparsely pilose with spreading hairs; lower culm blades 1–3 cm long ..... See 26D. *D. acuminatum* var. *implicatum*
  bb. Ligules 0.5 mm or less long; spikelets 1.1–2.9 mm long; sheaths and lower culm blades glabrous or rarely pilose with spreading hairs; lower culm blades short or long.
    c. Lower culm blades commonly more than 5 cm long or more than 4.5 mm broad; spikelets 1.5–2.4 mm long; plants widespread in eastern United States, in well-drained woodland sites ..... 24A. *D. dichotomum* var. *dichotomum*
    cc. Lower culm blades usually not more than 5 cm long and 4.5 (rarely 6) mm broad (but leaves of the basal rosette often much longer); spikelets 1.1–1.6 mm long; plants of moist seeps and acid bogs.
      d. Margins of blades thin, green; spikelets glabrous or sparsely puberulent ..... 24B. *D. dichotomum* var. *ensifolium*
      dd. Margins of blades with a cartilaginous, usually whitish border; spikelets puberulent ..... 24C. *D. dichotomum* var. *tenue*

aa. Blades of the lower culm leaves, at least some, 6–15 cm long but only 2–4 mm broad.
  e. Spikelets puberulent, 1.9–2 mm long; blades often 12–15 cm long ..... See 23. *D. aciculare*
  ee. Spikelets glabrous or pubescent, 1.2–1.5 mm long; blades to 6, occasionally to 8, cm long.

f. Spikelets glabrous, 1.2–1.5 mm long; blades glabrous ..... 24D. *D. dichotomum* var. *glabrifolium*

ff. Spikelets pubescent, (1.2–)1.3–1.4 mm long; blades with a few long, stiff hairs on the margins towards the base ..... 24E. *D. dichotomum* var. *breve*

24A. **D. dichotomum** (L.) Gould var. **dichotomum.**

SYNONYMS: ***Panicum nitidum*** Lamarck, 1791.
P. heterophyllum Muhlenberg, 1793.
P. nodiflorum Lamarck, 1798. Fragment and photo of holotype, US.
P. barbulatum Michaux, 1803. Fragment of lectotype, US.
P. microcarpon Muhlenberg ex Elliott, 1816.
P. angustifolium LeConte ex Torrey, 1818, not Elliott, 1816.
P. tremulum Sprengel, 1821. Fragment and photo of lectotype, US.
P. nitidum var. *barbatum* Torrey, 1824.
P. nitidum var. *ramulosum* Torrey, 1824.
P. dumus Desvaux, 1831.
P. dichotomum var. *nitidum* (Lamarck) Wood, 1861.
P. dichotomum var. *barbulatum* (Michaux) Wood, 1861.
P. dichotomum var. *nodiflorum* (Lamarck) Grisebach, 1866.
P. nudicaule Vasey, 1889. Lectotype, US; isolectotype, NY, TAES.
P. dichotomum var. *divaricatum* Vasey, 1889. Lectotype, US.
P. dichotomum var. *viride* Vasey, 1889. Lectotype, US.
P. nitidum var. *pauciflorum* Britton, 1889. Holotype, US.
P. nitidum var. *viride* (Vasey) Britton, 1889.
P. pubescens Lamarck var. *barbulatum* (Michaux) Britton, 1889.
P. dichotomum var. *commune* S. Watson & Coulter, 1890.
P. ramulosum Michaux ex Nash var. *viride* (Vasey) Porter, 1893.
P. sphagnicola Nash, 1895. Holotype, NY; isotypes, MO, NY, TAES, US.
P. nitidum var. *barbulatum* (Michaux) Chapman, 1897.
P. annulum Ashe, 1898, not A. Rich., 1851. Lectotype, US.
P. lucidum Ashe, 1898. Lectotype, US; isolectotype, NY.
P. maculatum Ashe, 1898, not Aublet, 1775.
P. mattamuskeetense Ashe, 1898. Isolectotypes, NY, US.
P. roanokense Ashe, 1898.
P. clutei Nash, 1899. Isotypes, NY, US.
P. curtivaginum Ashe, 1900.
P. taxodiorum Ashe, 1900. Holotype, NY; isotype, MO.
P. flexuosum Muhlenberg ex Scribner & Merrill, 1900, not Retzius, 1791. Holotype, US.
P. multirameum Scribner, 1900. Isotype, MO.
P. bogueanum Ashe, 1900.
P. yadkinense Ashe, 1900. Isolectotype, US.
P. subbarbulatum Scribner & Merrill, 1901.
P. gravius Hitchcock & Chase, 1906. Holotype, US.
P. caerulescens Hackel ex Hitchcock, 1909. Isotype, NY.
Chasea dichotoma (L.) Nieuwland, 1911.
Panicum mattamuskeetense var. *clutei* (Nash) Fernald, 1937.
P. lucidum var. *opacum* Fernald, 1937. Syntypes, MO, NY, US.
P. annulum var. *glabrescens* Gleason, 1952. Holotype, US.

Culms slender, 20–80(–110) cm tall, with glabrous internodes and glabrous or bearded nodes. *Sheaths* glabrous on the back, infrequently the lowermost ones velvety-pilose. *Blades* of the main culm leaves 4–12(–15) cm long, 3–10 (–13) mm broad, thin, usually glabrous on both surfaces but occasionally pilose, often sparsely ciliate on the margins near the base. *Leaves* of fascicled secondary branches with narrow, flat or involute blades, commonly 3–7 cm long as in *P. dichotomum* var. *tenue*, the blades occasionally with thick whitish margins. *Panicles* well-exserted, open, with the branches, branchlets, and pedicels tending to be spreading, the spikelets never appearing secund on the branches; *late-*

formed panicles greatly reduced, few-flowered. *Spikelets* elliptic or obovate, 1.5–2.9 mm long, glabrous or occasionally puberulent. *First glume* ca. ⅓ as long as the spikelet.

HABITAT AND DISTRIBUTION. In moist, sandy soil, usually in shaded, woodland habitats. Throughout eastern North America from Ontario, New Brunswick, Nova Scotia, Maine, and Michigan south to Florida, Missouri, Texas, and eastern Mexico.

24B. **D. dichotomum** (L.) Gould var. **ensifolium** (Baldwin) Gould & Clark, comb. nov. TYPE: Georgia, *Baldwin*. Fragment and photo of holotype, US.

BASIONYM: *Panicum ensifolium* Baldwin ex Elliott, Bot. S.C. & Ga. 1: 126. 1816.
SYNONYMS: *Panicum chamaelonche* Trinius, 1826. Fragment of holotype, US.
P. nitidum Lamarck var. *ensifolium* (Baldwin) Vasey, 1889.
P. flavovirens Nash, 1899. Isotype, NY.
P. ramulosum Michaux ex Nash, 1889. Fragment and photo of holotype, US.
P. nitidum var. *minus* Vasey, 1892. Holotype, US; isotype, MO.
P. baldwinii Nuttall ex Kearney, 1897. Holotype, US.
P. brittoni Nash, 1897. Syntypes, NY, US.
P. cuthbertii Ashe. 1898.
P. glabrissimum Ashe, 1898. Lectotype, US; isotypes, NY, US.
P. shallotte Ashe, 1900.
P. parvipaniculatum Ashe, 1900. Isolectotype, US.
P. vernale Hitchcock & Chase, 1910. Holotype, US.
Dichanthelium ensifolium (Baldwin) Gould, Brittonia 26: 59. 1974.

Culms slender and delicate, glabrous, 15–45 cm tall. *Sheaths* glabrous or minutely fringed on the margins. *Ligule* 0.5 mm or less long. *Blades* thin, short, spreading, often reflexed, glabrous or puberulent towards the tip. *Panicles* 2–6 cm long, the short, spreading branches with few spikelets. *Spikelets* broadly oblong or obovate, puberulent or glabrous, 1.1–1.5 mm long.

HABITAT AND DISTRIBUTION. In wet seeps, marshy areas and acid soils of bogs, usually in shade. Coastal Plain, New Jersey to Florida and Texas, also reported for Arkansas.

24C. **D. dichotomum** var. **tenue** (Muhl.) Gould & Clark, comb. et stat. nov. TYPE: No. 192 in the Muhlenberg Herb., PH. Fragment and photo of lectotype, US.

BASIONYM: *Panicum tenue* Muhlenberg, Descr. Gram. 118. 1817.
SYNONYMS: *Panicum deustum* Brickell & Enslin ex Muhlenberg, 1817, not Thunberg, 1794. Fragment and photo of holotype, US.
P. liton Schultes, 1824.
P. unciphyllum Trinius, 1826. Holotype, US.
P. macrum Kunth, 1829.
P. albomarginatum Nash, 1897. Holotype, NY; isotypes, MO, NY, US.
P. trifolium Nash, 1899. Holotype, NY; isotype, US.
P. parvulum Muhlenberg ex Scribner & Merrill, 1900, not Trinius, 1834.
P. gracilicaule Nash, 1903, not Rendle, 1899. Fragment and photo of holotype, US.
P. concinnius Hitchcock & Chase, 1910.

Culms typically delicate, 15–45 cm tall, glabrous or appressed-pubescent or pilose. *Ligules* minute, not over 0.5 mm long. *Blades* ascending or spreading, 2–5 cm long, 2–4 mm broad, usually rather thick, with thickened, whitish borders in "albomarginatum" types. *Spikelets* puberulent, elliptic, 1.3–1.6 mm long.

HABITAT AND DISTRIBUTION. In acid soils of bogs, wet seep and marshy area. Coastal Plain, Maryland to Georgia and Florida, and west to Texas; also in Mexico.

Although most plants with the general characteristics of *D. dichotomum* var. *tenue* conform to the characterization of the species as presented above, occasionally the basal blades and lower culm leaves are unusually large, sometimes as much as 10 cm long and 10 mm broad.

24D. **D. dichotomum** (L.) Gould var. **glabrifolium** (Nash) Gould & Clark, comb. et stat. nov. TYPE: Florida, in "flatwoods" at Tampa, *Nash 2415a*. Holotype, NY.

BASIONYM: *Panicum glabrifolium* Nash, Bull. Torrey Bot. Club 24: 196. 1897. Fragment and photo of holotype, US.

Plants tufted, 15–50 cm tall. *Blades* firm, 4–12 cm long, 2–4 mm broad. *Panicles* open, 4–9 cm long. *Spikelets* 1.2–1.4 mm long, broadly obovate, glabrous, 1.2–1.4 mm long.

HABITAT AND DISTRIBUTION. Infrequent in low, moist, sandy woods. Southern Florida (Polk and Hillsborough counties and south).

24E. **D. dichotomum** (L.) Gould var. **breve** (Hitchcock & Chase) Gould & Clark, comb. et stat. nov. TYPE: Florida, Jensen, *Hitchcock 734*. Holotype, US.

BASIONYM: *Panicum breve* Hitchcock & Chase, Contr. U.S. Natl. Herb. 15: 27. 1910.

Plants low, tufted, 5–20 cm tall. *Culms* wiry, glabrous or appressed-pubescent below. *Sheaths* ciliate on the margins, glabrous on the back. *Ligule* a ring of hairs ca. 0.3 mm long. *Blades* firm, 3–6(–8) cm long, ca. 1.5 mm broad, strongly involute and more or less falcate, with a few long, stiff hairs on the margins towards the base. *Panicles* short-exserted, 1.5–4 cm long, loosely flowered. *Spikelets* broadly obovate, puberulent, 1.3–1.4 mm long.

HABITAT AND DISTRIBUTION. In low, moist, pine and scrub hardwood woods. Southern Florida (Polk Co. and south).

25. **D. boreale** (Nash) Freckmann, Phytologia 39: 269. 1978. TYPE: New York, Green Co., Cairo, *G. V. Nash* in 1893. Holotype, NY; isotype, NY.

BASIONYM: *Panicum boreale* Nash, Bull. Torrey Bot. Club 22: 421. 1895.
SYNONYMS: *Panicum boreale* var. *michiganense* Farwell, 1940. Holotype, US.
P. bicknellii Nash, 1897. Isolectotype, US.
P. calliphyllum Ashe, 1898. Lectotype, US; isolectotype, NY.
P. bushii Nash, 1899.
P. bicknellii var. *bushii* (Nash) Farwell, 1921.

Culms slender, stiffly erect, glabrous or the lowermost nodes puberulent, mostly 25–60 cm tall but plants frequently flowering when only 10–15 cm tall, little-branched above the base, the secondary branches when present with relatively large leaves and broad blades. *Sheaths* glabrous or the lowermost finely

pilose, usually ciliate with soft hairs on the margins, and often with tufts of soft hair on either side just below the ligular region. *Ligule* absent or a ring of short hairs not over 1 mm long. *Blades* tending to be glabrous, thin, broad and erect, mostly 6–14 cm long and 6–13 mm broad, the lower blades when long usually broadest at the middle and narrowing to a cordate or subcordate base. *Blade base* typically ciliate with few, long papilla-based hairs, the hairs occasionally present to above the middle. *Panicles* open, few-flowered 5–8(–9) cm long, the main panicle axis and branches glabrous. *Spikelets* glabrous or pubescent, elliptic or slightly elliptic-obovate, 2.0–2.8 mm long, the tips of the second glume and lemma of the lower floret typically pointed. *First glume* broad, ¼–⅓ as long as the spikelet.

HABITAT AND DISTRIBUTION. In woodlands and on open grassy slopes, usually in moist soil. Newfoundland, Quebec, and Ontario, south to North Carolina, Indiana, Michigan, and Minnesota.

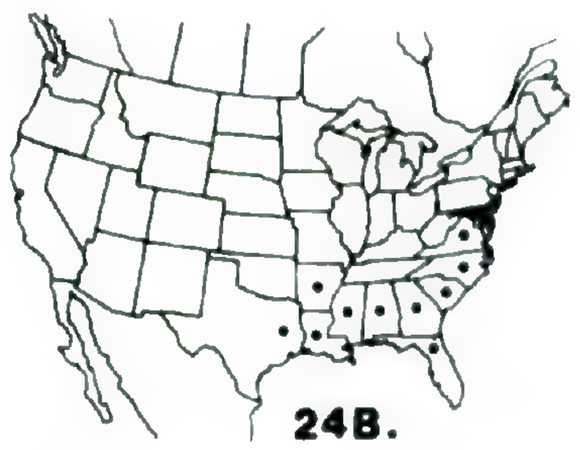
Dichanthelium boreale appears to be close to and possibly intergrading with *D. dichotomum* var. *dichotomum* and *D. commutatum*. Perhaps most typical of the species are plants with stiffly erect culms 30–45 cm tall and short, broad, stiffly erect blades. Included in the taxon, however, are relatively tall, slender plants with low internodes and long, broad, loosely erect-spreading blades that approach *D. dichotomum* var. *dichotomum* in general aspect but do not develop fascicles of reduced branchlets. These plants have for the most part been referred to *Panicum bicknellii* Nash and *P. calliphyllum* Ashe. *D. boreale* is little-branched at the upper nodes and does not develop fascicles of reduced leaves and inflorescences as in *D. dichotomum*.

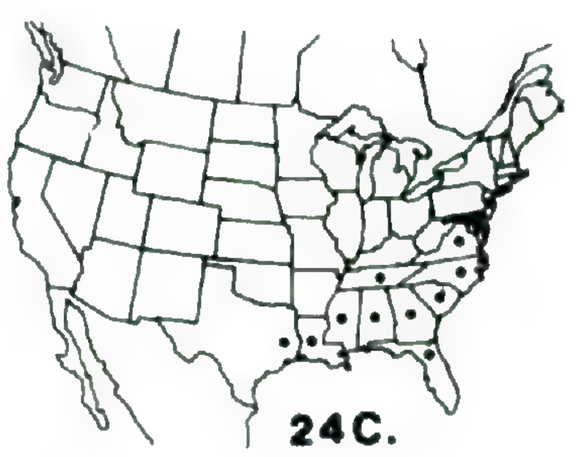
26. **D. acuminatum** (Swartz) Gould & Clark, comb. nov. TYPE: Jamaica, *Swartz*. Fragment and photo of holotype, US.

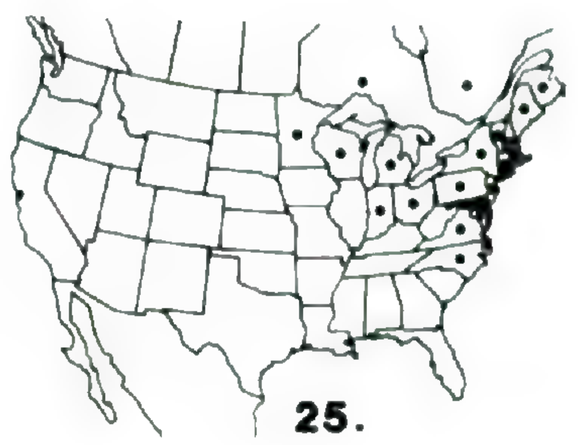
BASIONYM: *Panicum acuminatum* Swartz, Prodr. Veg. Ind. Occ. 25. 1788.

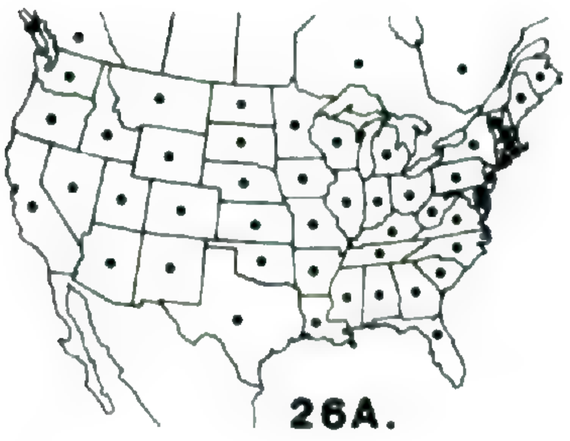
Plants with a well-developed rosette of broad, short basal leaves. *Culms* 15–70(–80) cm tall, usually becoming much-branched in age and commonly forming mats or pads of reduced branches and small, few-flowered panicles, the nodes and internodes glabrous or more commonly hairy. *Ligular hairs* well-developed, mostly 2–5 mm long but as short as 1 mm long in var. *implicatum*. *Leaves* glabrous to variously hairy. *Panicles* open or somewhat contracted, 2–12 cm long. *Spikelets* ovate, elliptic or slightly obovate, glabrous or more commonly pubescent, 0.8–2.7 mm long. *First glume* broad, rounded or abruptly pointed, ⅕–⅓ as long as the spikelet.

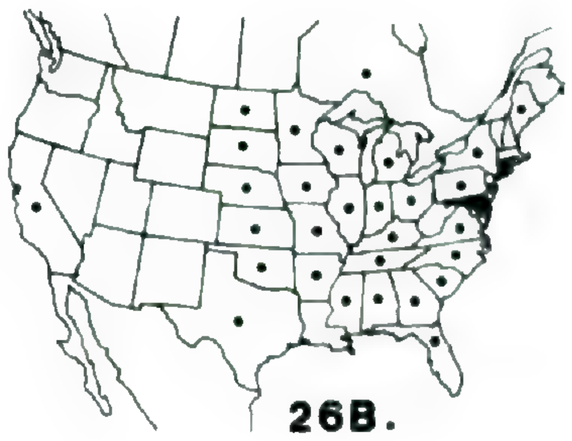
In the following treatment, the populations referred to *D. acuminatum* are grouped into eight varieties. Listed as synonyms of the varietal names are a total of 46 names, many of which have been treated variously as species or varieties. It may be that the taxa retained as varieties do not adequately delimit the recognizable populations of this extremely widely distributed and morphologically variable species. The present treatment, however, provides a basis for

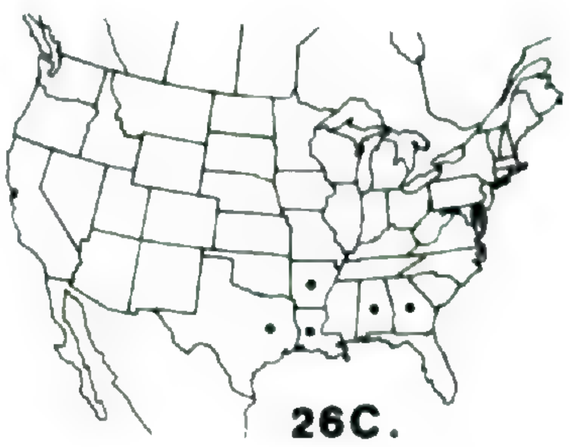


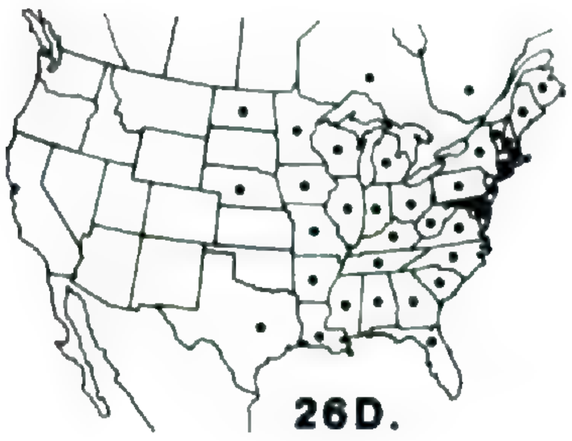


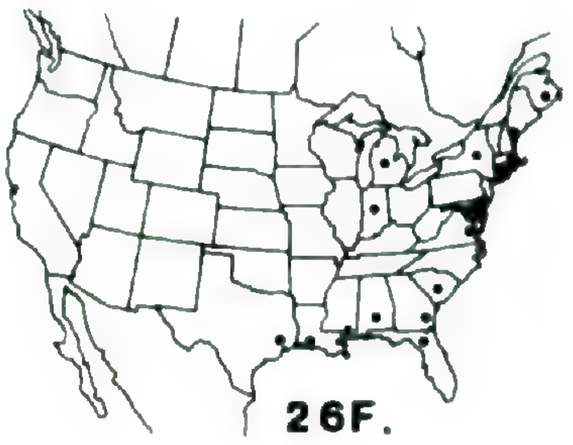












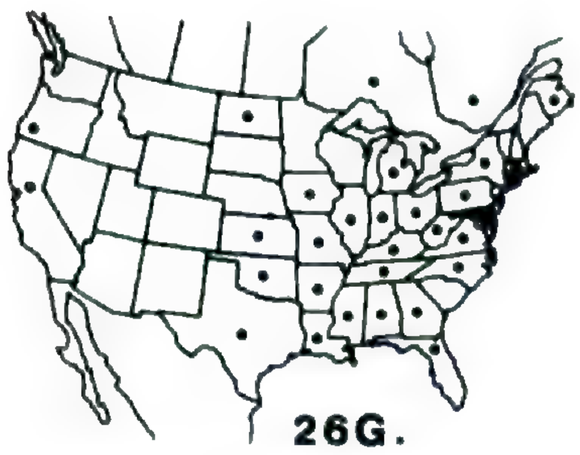


FIGURE 3. 24A. *D. dichotomum* var. *dichotomum*. 24B. *D. dichotomum* var. *ensifolium*. 24C. *D. dichotomum* var. *tenue*. 24D. *D. dichotomum* var. *glabrifolium*. 24E. *D. dichotomum* var. *breve*. 25. *D. boreale*. 26A. *D. acuminatum* var. *acuminatum*. 26B. *D. acuminatum* var. *villosum*. 26C. *D. acuminatum* var. *thurowii*. 26D. *D. acuminatum* var. *implicatum*. 26E. *D. acuminatum* var. *wrightianum*. 26F. *D. acuminatum* var. *densiflorum*. 26G. *D. acuminatum* var. *longiligulatum*. 26G. *D. acuminatum* var. *lindheimeri*.

comparative treatments of populations segregated mainly on the basis of spikelet size and type of indument.

Key to the varieties

a. Culms pubescent or hairy; sheaths of culm leaves, at least the lower ones, puberulent, pubescent, hirsute or villous on the back.

b. Sheaths with soft, spreading or reflexed hairs 2–5 mm long; spikelets 1.8–2.7 mm long ..... 26B. *D. acuminatum* var. *villosum*
bb. Sheath hairs stiff or soft, ascending or erect-appressed, usually less than 2 mm long; spikelets 0.8–2.5 mm long.
c. Spikelets 1.6–2.5 mm long.
d. Culms not robust, mostly 15–60 cm tall; panicles broad, open, rarely over 8 cm long ..... 26A. *D. acuminatum* var. *acuminatum*
dd. Culms robust, mostly 50–70 cm or more tall; panicle commonly narrow and somewhat contracted, 9–12 cm long ..... 26C. *D. acuminatum* var. *thurowii*
cc. Spikelets 0.8–1.5 long.
e. Spikelets 1.2–1.5 mm long ..... 26D. *D. acuminatum* var. *implicatum*
ee. Spikelets 0.8–1.1 mm long ..... 26E. *D. acuminatum* var. *wrightianum*
aa. Culms glabrous or the lower portions slightly hairy; sheaths glabrous or the lowermost sheaths sparsely pilose or puberulent on the back.
f. Spikelets 1.4–1.8 mm long.
g. Panicle narrow, ¼–⅓ as broad as long, commonly 8–12 cm long ..... 26F. *D. acuminatum* var. *densiflorum*
gg. Panicle broad, ⅔ to nearly as broad as long, commonly 5–8 cm long ..... 26G. *D. acuminatum* var. *lindheimeri*
ff. Spikelets 1.1–1.3 mm long ..... 26H. *D. acuminatum* var. *longiligulatum*

26A. **D. acuminatum** (Swartz) Gould & Clark var. **acuminatum**.

SYNONYMS: *Panicum lanuginosum* Elliott, 1816. Fragment and photo of holotype, US.
P. nitidum Lamarck var. *ciliatum* Torrey, 1824.
P. dichotomum (L.) var. *fasciculatum* Torrey, 1824.
P. nitidum var. *pilosum* Torrey, 1824.
P. dichotomum var. *pubescens* Munro ex Bentham, 1857.
P. dichotomum var. *lanuginosum* (Elliott) Wood, 1861.
P. thermale Bolander, 1862. Isotypes, MO.
P. tennesseense Ashe, 1898. Fragment and photo of holotype, US.
P. huachucae Ashe, 1898. Lectotype, US.
P. scoparioides Ashe, 1898. Lectotype, US; isolectotypes, NY.
P. occidentale Scribner, 1899. Isotype, MO.
P. orangense Ashe, 1899.
P. ciliosum Nash, 1899. Holotype, NY; isotype, US.
P. subvillosum Ashe, 1900. Fragment and photo of holotype, US.
P. unciphyllum Trinius f. *pilosum* Scribner & Merrill, 1901.
P. unciphyllum f. *prostratum* Scribner & Merrill, 1901, not *P. prostratum* Lamarck.
P. shastense Scribner & Merrill, 1901.
P. chrysopsidifolium Nash, 1903. Isotype, NY.
P. comophyllum Nash, 1903. Holotype, NY.
P. lanuginosum var. *huachucae* (Ashe) Hitchcock, 1906.
P. huachucae var. *silvicola* Hitchcock & Chase, 1908. Holotype, US.
P. pacificum Hitchcock & Chase, 1910. Isotype, NY.
P. languidum Hitchcock & Chase, 1910.
P. huachucae var. *fasciculatum* (Torrey) Hubbard, 1912.
P. lindheimeri Nash var. *fasciculatum* (Torrey) Fernald, 1921.
P. lindheimeri var. *septentrionale* Fernald, 1921.
P. lindheimeri var. *tennesseense* (Ashe) Farwell, 1928.
P. lanuginosum var. *septentrionale* (Fernald) Fernald, 1934.
P. lanuginosum var. *fasciculatum* (Torrey) Fernald, 1934.
P. villosissimum Nash var. *scoparioides* (Ashe) Fernald, 1934.
P. brodiei St. John, 1937.
P. lassenianum Schmoll, 1939.
P. ferventicola Schmoll, 1939. Isotype, NY.
P. ferventicola var. *papillosum* Schmoll, 1939. Isotype, NY.
P. ferventicola var. *sericeum* Schmoll, 1939. Isotype, NY.
P. benneri Fernald, 1944. Holotype(?), US.
P. glutinoscabrum Fernald, 1947.

P. lanuginosum var. *tennesseense* (Ashe) Gleason, 1952.
Dichanthelium lanuginosum (Elliott) Gould, Brittonia 26: 60. 1974.
D. lanuginosum var. *fasciculatum* (Torrey) Spellenberg, Madroño 23: 145. 1975.
D. lanuginosum var. *sericeum* (Schmoll) Spellenberg, Madroño 23: 150. 1975.
D. lanuginosum var. *thermale* (Bolander) Spellenberg, Madroño 23:151. 1975.

Culms usually in large clumps, 15–60 cm tall, usually densely villous below with long, soft hairs, these often minutely papillate. *Leaves* variously pubescent to nearly glabrous, the hairs soft or coarse, usually long. *Sheaths* shorter than the internodes, soft-villous or puberulent on the back, ciliate on the margins. *Ligules* well developed with hairs mostly 2–4 mm long. *Blades* thickened as in var. *implicatum* but not stiff, mostly 5–10 cm long and 5–10(–12) mm broad, the adaxial surface usually with long hairs or short and long soft hairs intermixed, the abaxial surface densely, velvety-pubescent to nearly glabrous. *Panicles* 5–8 cm long, loosely-flowered, commonly pubescent on the main axis and lower branches. *Spikelets* pubescent, elliptic-obovate, 1.6–2.5 mm long. *First glume* about as broad as long, ⅓ as long as the spikelet, broadly pointed to somewhat rounded at the apex.

HABITAT AND DISTRIBUTION. In a wide variety of habitats, mostly in moist, sandy soil of woodlands and woods borders. Widespread throughout North America from Quebec and British Columbia to Florida, California and eastern Mexico; also in Central America, the Antilles, and northern South America, and adventive in the Hawaiian Islands.

In the present interpretation, *D. acuminatum* var. *acuminatum* is arbitrarily separated from *D. acuminatum* var. *implicatum* on the basis of spikelet size (1.6–2.5 vs. 1.2–1.5). The culms and leaves of var. *implicatum* do tend to be smaller than those of var. *acuminatum* but no satisfactory separation can be made on this basis.

Lelong (1965) followed Chase in Hitchcock (1951) in recognizing *Panicum scoparioides* as a distinct species and treated *P. benneri*, *P. shastense*, and *P. villosissimum* var. *scoparioides* as synonyms. The characteristics upon which the *scoparioides* taxon is based do not appear sufficiently distinctive nor consistent to warrant taxonomic recognition. Lelong had doubts as to the validity of *P. scoparioides* as a species and stated (Lelong, 1965: 195),

> . . . that this "rare species" is merely another resulting variant from sporadic hybridization between *P. scribnerianum* and western forms of *P. lanuginosum* (such as *Heller 12452* identified as *P. pacificum*). Until it can be ascertained that *P. shastense* is indeed a rare hybrid, it should probably be regarded as a synonym of *P. scoparioides*. The surprisingly great similarity between western and eastern Lanuginosa has already been noted.

26B. **D. acuminatum** (Swartz) Gould & Clark var. **villosum** (A. Gray) Gould & Clark, comb. nov. TYPE: New York, Ontario Co., *Sartwell*?

BASIONYM: *Panicum nitidum* Lamarck var. *villosum* A. Gray, N. Amer. Gram. & Cyp. 2: 111. 1835.
SYNONYMS: *Panicum tectum* Willd. ex Sprengel, 1825.
P. dichotomum L. var. *villosum* (A. Gray) Vasey, 1889. Lectotype, US.
P. nitidum var. *pubescens* Scribner, 1893. Isotypes(?), NY.
P. laxiflorum Lamarck var. *pubescens* Chapman, 1893, not Vasey, 1892. Lectotype, US.
P. villosissimum Nash, 1896. Holotype, NY; isotypes, NY, US.

P. atlanticum Nash, 1897. Holotype, NY; isotype, US.
P. haemacarpon Ashe, 1898. Lectotype, NY; isolectotype, US.
P. pseudopubescens Nash, 1899. Holotype(?), NY.
P. cahoonianum Ashe, 1899. Isotypes, NY.
P. xanthospermum Scribner & Mohr, 1901. Holotype, US.
P. praecocius Hitchcock & Chase, 1906. Holotype, US; isotype, NY.
P. olivaceum Hitchcock & Chase, 1910.
P. villosissimum var. *pseudopubescens* Fernald, 1934.
P. euchlamydeum Shinners, 1944. Isotype, US.
Dichanthelium lanuginosum (Elliott) Gould var. *villosissimum* (Nash) Gould, Brittonia 26: 60. 1974.
Panicum lanuginosum var. *praecocius* (Hitchcock & Chase) McNeill & Dore, Naturaliste Canad. 103. 1976.
Dichanthelium villosissimum (Nash) Freckmann, Phytologia 39: 270. 1978.
D. villossimum (Nash) Freckmann var. *praecocius* (Hitchcock & Chase) Freckmann, Phytologia 39: 270. 1978.

Plants mostly 20–60 cm tall. *Culm nodes* bearded with long, soft, spreading hairs. *Sheath* villous with papilla-based hairs, 2–5 mm long, these spreading or reflexed on at least some sheaths. *Ligules* usually with hairs 3–5 mm long, occasionally some of the lateral hairs 1 mm or less long. *Blades* 6–10 cm long and 5–10 mm broad, usually pilose on both surfaces, the adaxial surface with hairs 2–4 mm long. *Spikelets* puberulent, elliptic, 1.8–2.7 mm long.

HABITAT AND DISTRIBUTION. Woods and woods borders, brushy or recently cleared pastures, usually in sandy soil. Throughout the eastern half of the United States, Connecticut and New York south to Florida and west to Minnesota, Nebraska, Kansas, Texas, and California; also eastern Mexico.

Plants in the northern part of the range with relatively small spikelets (1.8–2.4 mm long) and leaf surfaces tending to be papillate-strigose rather than villous have commonly been referred to *Panicum praecocius* Hitchcock & Chase.

Gray, in proposing the name *Panicum nitidum* var. *villosum*, listed in synonymy "*P. pubescens* Lam'k. Enc. Meth. IV. p. 748? Muhl. Gram. p. 116?" Hitchcock & Chase (1910) list *Panicum pubescens* Lamarck as a synonym of *P. scoparium* Lamarck.

26C. **D. acuminatum** (Swartz) Gould & Clark var. **thurowii** (Scribner & Smith) Gould & Clark, comb. et stat. nov. TYPE: Texas, Waller Co., *F. W. Thurow 9*. Holotype, US.

BASIONYM: *Panicum thurowii* Scribner & Smith, U.S.D.A. Div. Agrost. Circ. 16: 5. 1899. Holotype, US.

Culms stout, 40–70(–80) cm tall, with well-spaced nodes, the nodes bearded with spreading hairs, usually with a glabrous ring below. *Sheaths* densely to sparsely villous. *Ligule* a dense ring of hairs 3–4 mm long. *Blades* 7–12 cm long, 6–10 mm broad, velvety-villous on the abaxial surface, the adaxial surface more or less pilose. *Panicles* 9–11 cm long. *Spikelets* elliptic-obovate, pubescent, 1.8–2 mm long, rounded or broadly pointed at the apex. *First glume* very short and broad, ⅛–¼ as long as the spikelet.

HABITAT AND DISTRIBUTION. In dry woods, woods borders and brushy pastures. Occasional in Georgia, Alabama, Arkansas, Louisiana, and eastern Texas.

26D. **D. acuminatum** (Swartz) Gould & Clark var. **implicatum** (Scribner) Gould & Clark, comb. nov. TYPE: Maine, Cape Elizabeth, *F. Lamson-Scribner* in 1895. Holotype, US; isotype, NY.

BASIONYM: *Panicum implicatum* Scribner, U.S.D.A. Dept. Agr. Div. Agrost. Bull. 11: 43. 1898. Holotype, US; isotype, NY.
SYNONYMS: *Panicum velutinum* Bosc, 1825, not Meyer, 1818.
P. leucothrix Nash, 1897. Holotype, NY; isotypes, NY, TAES, US.
P. parvispiculum Nash, 1897. Holotype, NY, fragment and photo of holotype, US; isotypes, NY.
P. microphyllum Ashe, 1898. Isolectotypes, NY, US.
P. meridionale Ashe, 1898. Lectotype, US.
P. filiculme Ashe, 1898.
P. curtifolium Nash, 1899. Holotype, NY.
P. earlei Nash, 1899. Holotype, NY.
P. albemarlense Ashe, 1900. Lectotype, US.
P. auburne Ashe, 1900.
P. austro-montanum Ashe, 1900.
P. unciphyllum Trinius var. *implicatum* (Scribner) Scribner & Merrill, 1901.
P. unciphyllum var. *meridionale* (Ashe) Scribner & Merrill, 1901.
P. lindheimeri Nash var. *implicatum* subvar. *meridionale* (Ashe) Farwell, 1928.
P. meridionale var. *albermarlense* (Ashe) Fernald, 1934.
P. lanuginosum Elliott var. *implicatum* (Scribner) Fernald, 1934.
P. lanuginosum var. *implicatum* subvar. *meridionale* (Ashe) Farwell, 1941.
Dichanthelium meridionale (Ashe) Freckmann, Phytologia 39: 270. 1978.

Culms 10–60(–70) cm tall, pilose on the lower internodes, the nodes puberulent. *Sheaths*, at least the lower ones, puberulent or papillose-pilose. *Ligules* 1–5 mm long. *Blades* firm, strigose or puberulent to nearly glabrous on the surfaces, often with a few long hairs interspersed with the short ones, mostly 2–6 cm long and 2–5 mm broad. *Spikelets* puberulent, elliptic to subspherical, slightly pointed, 1.2–1.5 mm long. *First glume* broad, about ¼ as long as the spikelet.

HABITAT AND DISTRIBUTION. In sandy woodlands and cleared woodland areas, occasionally in low, marshy, pine, cedar, and hemlock forest. Nova Scotia, New Brunswick, Quebec, Ontario, Maine, New York, Michigan, Wisconsin, Minnesota, North Dakota, Nebraska, and south to Florida and Texas; also in Cuba.

26E. **D. acuminatum** (Swartz) Gould & Clark var. **wrightianum** (Scribner) Gould & Clark, comb. et stat. nov. TYPE: Cuba, *C. Wright 3463*. Holotype, US; isotype, MO.

BASIONYM: *Panicum wrightianum* Scribner, U.S.D.A. Div. Agrost. Bull. 11: 44. *fig. 4.* 1898.
SYNONYMS: *Panicum strictum* Bosc ex Roemer & Schultes, 1817, not R. Br., 1810.
P. minutulum Desvaux, 1833, not Gaudin, 1826.
P. deminutivum Peck, 1907. Holotype, NY; isotypes, US.

Culms slender, weak, usually decumbent at the base, minutely puberulent at least on the lower internodes, 15–40(–50) cm tall. *Sheaths* shorter than the internodes, glabrous or puberulent on the back, ciliate on the margins and on the sides of the collar. *Blades* usually puberulent to pilose on both surfaces. *Panicles* open, 3–6 cm long, the minute spikelets long-pediceled. *Spikelets* puberulent, elliptic, pointed at the apex, ca. 1 mm long.

HABITAT AND DISTRIBUTION. In moist, sandy or muddy swamps, swales, and

boggy shorelines. Along the Coastal Plain, Massachusetts and New York to Florida and west to Louisiana and Texas.

26F. **D. acuminatum** (Swartz) Gould & Clark var. **densiflorum** (Rand & Redfield) Gould & Clark, comb. nov. TYPE: Maine. Mt. Desert shore of Ripples Pond, *Rand* in 1892.

BASIONYM: *Panicum nitidum* Lamarck var. *densiflorum* Rand & Redfield, Fl. Mt. Desert 174. 1894.
SYNONYMS: *Panicum spretum* Schultes, 1824.
P. eatoni Nash, 1898. Holotype, NY.
P. octonodum Smith, 1899. Isotypes, NY, US.
P. paucipilum Nash, 1899. Holotype, NY; isotypes, NY, US.
P. nitidum var. *octonodum* (Smith) Scribner & Merrill, 1901.

Sheaths glabrous on the back or the lower ones occasionally slightly puberulent, the margins usually ciliate above. *Ligules* usually 2–3 mm long. *Blades of culm leaves* 7–10 cm long, 4–8 mm broad, usually long-ciliate at the rounded base. *Panicle* 7–12 cm long, ¼–⅓ as broad as long, relatively many-flowered. *Spikelets* puberulent, elliptic, broadly pointed, 1.4–1.8 mm long. *First glume* very short.

HABITAT AND DISTRIBUTION. Usually in moist, sandy soil. Occasional on the Coastal Plain, Maine to northern Florida, Louisiana, and eastern Texas.

26G. **D. acuminatum** (Swartz) Gould & Clark var. **lindheimeri** (Nash) Gould & Clark, comb. nov. TYPE: Texas, Comal Co., New Braunfels, *Lindheimer* 565. Holotype, NY; isotypes, MO, NY.

BASIONYM: *Panicum lindheimeri* Nash, Bull. Torrey Bot. Club 24: 196. 1897.
SYNONYMS: *Panicum funstoni* Scribner & Merrill, 1901. Holotype, US.
P. lindheimeri var. *typicum* Fernald, 1921.
P. lanuginosum Elliott var. *lindheimeri* (Nash) Fernald, 1934.
Dichanthelium lindheimeri (Nash) Gould, Brittonia 26: 60. 1974.
D. lanuginosum var. *lindheimeri* (Nash) Freckmann, Phytologia 39: 270. 1978.

Culms slender, 30–70(–90) cm tall, glabrous or the internodes sparsely pilose, soon "bushy-branched" at the upper nodes to produce fascicles of small inflorescences. *Sheaths* glabrous on the back, glabrous or pilose on the margins. *Ligules* dense, 2–5 mm long. *Blades* bright green, glabrous or essentially so, 3–9(–15) cm long and 3–11 mm broad. *Panicles* open, 4–7(–10) cm long. *Spikelets* puberulent, elliptic or slightly obovate, 1–2 mm long.

HABITAT AND DISTRIBUTION. This grass usually is in woodlands and along woods borders, but also grows on open roadsides and in open pastures. Widespread throughout eastern and central North America, from southern New Brunswick, Ontario, and Manitoba southward, but absent or infrequent west of eastern Iowa, Kansas, and Oklahoma; a few records from Oregon, California and northeastern Mexico. It is common throughout the eastern two-thirds of Texas.

26H. **D. acuminatum** (Swartz) Gould & Clark var. **longiligulatum** (Nash) Gould & Clark, comb. et stat. nov. TYPE: Florida, Apalachicola, *Vasey*, 1892. Holotype, NY.

BASIONYM: *Panicum longiligulatum* Nash, Bull. Torrey Bot. Club 26: 574. 1899.

Culms glabrous, usually stout, to 70 cm tall. *Sheaths* glabrous on the back, often ciliate on the margins. *Ligules* 2–3 mm long. *Blades* rather thick, glabrous on the adaxial surface, puberulent on the abaxial surface, 4–8 cm long, 4–8 mm broad. *Spikelets* puberulent, elliptic, 1.1–1.3 mm long, rounded or broadly pointed at the apex. *First glume* about ¼ as long as the spikelet.

HABITAT AND DISTRIBUTION. Coastal Plain, Pennsylvania and New Jersey to Florida; also in Tennessee and eastern Texas.

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webberianum 1113
werneri 1098
wilcoxianum 1107
wilmingtonense 1115
wrightianum 1126
xalapense 1099
—var. *strictirameum* 1099
xanthospermum 1124
xanthosphysum 1108
—f. *amplifolium* 1108
yadkinense 1118

A SYSTEMATIC STUDY OF THE GENUS *LASIACIS* (GRAMINEAE: PANICEAE)[1, 2, 3]

GERRIT DAVIDSE[4]

ABSTRACT

A systematic treatment of the tropical American grass genus *Lasiacis* is presented. The gross morphology of *Lasiacis* is discussed. *Lasiacis* is panicoid in the form of its leaves, its roots, and its seedlings. Leaf anatomy was studied from cross-sections of blades and from the epidermis. *Lasiacis* has a typically non-Kranz (C_3) panicoid anatomy. It possesses the following major anatomical characteristics: three types of vascular bundles, angular secondary vascular bundles, partially radiate chlorenchyma around the vascular bundles, differentiated palisade and spongy chlorenchyma, double bundle sheaths around the primary vascular bundles, single parenchyma sheaths around the primary vascular bundles, single parenchyma sheaths around the secondary vascular bundles, short cells of costal zones in long rows, dumbbell and nodular silica bodies, bicellular microhairs, and triangular to dome-shaped subsidiary cells. The breeding system is predominantly inbreeding with a smaller amount of outbreeding. All species tested are self-compatible. New chromosome counts of $n = 18$ and $2n = 36$ are reported for 101 collections representing 13 species and 8 varieties. Reported for the first time are: *L. anomala*, *L. divaricata* var. *divaricata*, *L. harrisii*, *L. linearis*, *L. oaxacensis* var. *oaxacensis* and var. *maxoni*, *L. procerrima*, *L. ruscifolia* var. *velutina*, *L. sloanei*, *L. sorghoidea* var. *sorghoidea* and var. *patentiflora*, and *L. standleyi*. Meiosis was completely regular. In the taxonomic treatment, 23 taxa are recognized including 16 species and 13 varieties. A key to the species is provided. Synonymy, descriptions, discussions, distribution, ecology, common names, economic uses, and herbarium specimens are given for each species.

Lasiacis is a small neotropical grass genus of 16 species distributed from the southern tip of Florida and central Mexico south through the West Indies, Central America, and in South America to southern Peru and northern Argentina. Many species are rather striking in appearance because of their large, erect, woody culms. However, an almost equal number of species have procumbent, creeping, herbaceous culms. As striking are the shiny, black mature spikelets.

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[1] Based on a Ph.D. dissertation submitted to the Graduate College of Iowa State University, Ames, Iowa.

[2] I sincerely thank Dr. Richard W. Pohl for his support, advice, and helpful criticism throughout this study and in matters nonbotanical. I also thank Drs. D. Isely, J. L. Laffoon, N. R. Lersten, and K. Sadanaga, for critically reviewing the original dissertation and assisting in other ways. Appreciation is extended to the following persons who have helped me in various ways: Dr. T. R. Soderstrom, Smithsonian Institution; Dr. A. Lourteig, Muséum National d'Histoire Naturelle; Dr. E. McWilliams, Univ. of Michigan; Mr. C. Quarín, Univ. Nacional del Nordeste, Corrientes; Dr. M. T. Stiever, Carnegie-Mellon Univ., Pittsburgh; Dr. E. C. Tenorio, Univ. Federal Rural de Pernambuco; Dr. P. Weatherwax, Indiana Univ.; Dr. S. J. Goodband, Univ. of the West Indies, Trinidad; Dr. Jiménez, Dominican Republic; Ing. C. Blanco, Venezuela; Dr. Z. Luces de Febres and Dr. J. A. Steyermark, Instituto Botánico, Caracas; Drs. V. M. Badillo and L. Fernández, Univ. Central de Venezuela, Maracay; Dr. G. S. Bunting, Jardin Botánico, Maracaibo; Dr. G. R. Proctor, Institute of Jamaica; Mr. E. Conroy, Florida Atlantic Univ.; Dr. W. T. Stearn and Dr. E. Launert, British Museum of Natural History, London. I thank the curators of the herbaria listed in METHODS AND MATERIALS for providing specimens. I thank my wife, Jeany Vander Neut Davidse, for her support and encouragement during this study.

[3] Portions of the fieldwork were supported by Organization for Tropical Studies Grant F-70-26, N.S.F. Grants for Improving Doctoral Dissertation Research in the Field Sciences, GB-40630, and INT 76-14750 to Davidse, and Grants GB-7307 and GB-7307X to Pohl.

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ANN. MISSOURI BOT. GARD. 65: 1133–1254. 1978.

0026-6493/1133-1254/$12.25/0

All species are of little or no economic importance.

Lasiacis was first delimited as a section of *Panicum* (Grisebach, 1864). Hitchcock subsequently elevated the section to a genus (Hitchcock & Chase, 1910). This was followed by a treatment of all species north of Colombia (Hitchcock, 1920). This revision has continued to form a solid basis for later work in *Lasiacis*. Since Hitchcock's 1920 revision, published later in very similar form in *North American Flora* (Hitchcock, 1931), most systematic work with *Lasiacis* has been limited to regional floristic treatments, new species descriptions, and species transfers. The most important of these contributions were made by Hitchcock (1930, 1936), Parodi (1943), Swallen (1934, 1936, 1943, 1955a, 1955b, 1957), and Davidse (1974, 1977). Davidse & Morton (1973) reported on fruit dispersal, presenting evidence that the black spikelets are an adaptation to bird dispersal.

Systems of grass classification at the tribe and subfamily level traditionally relied largely on gross morphological features of the spikelets and inflorescences during the early part of this century. In recent years classifications have in addition been built on anatomical, cytological, physiological, and a wider array of gross morphological characters. Significant in the use of such a wide array of characters in constructing a system of grass classification was the pioneer effort of Avdulov (1931). He used size and base number of chromosomes, leaf anatomy, size and position of first seedling leaves, type of starch grains, and the type of nucleoli in nondividing cells to propose a new system of classification. Important among the new systems of classification that have used these characters are those of Prat (1960), Parodi (1961), and Stebbins & Crampton (1961). Although differing in detail, these authors agreed in recognizing six subfamilies (Bambusoideae, Oryzoideae, Arundinoideae, Pooideae, Chloridoideae, and Panicoideae). These new systems are phylogenetic and undoubtedly reflect genetic relationships much better than previous systems. The broad outlines of this new system seems rather stable at the present time.

There are many genera for which the new characters are not or only partially known, and these genera are placed in tribes and subfamilies strictly on the basis of spikelet and inflorescence structure. *Lasiacis* is such a genus. *Lasiacis* also has never been monographed in its entirety, nor have any biosystematic studies ever been made. In the following pages a complete systematic study of the genus is presented. A paper on hybridization will be published separately.

METHODS AND MATERIALS

This paper is based on studies in the herbarium, field, greenhouse, and laboratory.

Since *Lasiacis* has been rather extensively collected, complete collections were borrowed only from the major herbaria marked by an asterisk in the following list. Collections in other herbaria were studied in situ or specialized collections were borrowed. The herbaria are cited according to Holmgren & Keuken (1974): A, AWH, C, DS, EAP, F*, GH*, GOET, IJ, ISC*, K, L, MEXU*, M, MO*, MY*, NY*, P, RB*, SCZ, TRIN, UC*, US*, VEN*, WIS. Voucher specimens mentioned in this paper are deposited as ISC, and partial sets are also

deposited at MO and US. The abbreviations preceding collection numbers stand for the following collectors: *D* = Davidse, *E* = Erickson, *P* = Pohl.

Greenhouse Studies

Initially some difficulty was experienced in growing the various species in the greenhouse, mainly because of overwatering. The following procedure, with several exceptions, gave quite satisfactory results. Caryopses were dehulled (fertile lemma and palea removed), placed on blotters in petri dishes maintained at about 30°C, and watered as needed with distilled water. Dehulling speeded germination 10- to 20-fold. After the first or second leaf developed, seedlings were transferred to small pots with an equal mixture of peat moss and soil. Moderate watering with fortnightly to monthly liquid fertilizer applications encouraged normal growth.

Growth of the creeping species and *L. procerrima* in the greenhouse was best in a cool (ca. 21°C), plastic-enclosed humidity chamber containing a peat moss-soil mixture which allowed the stems to root at the nodes as they advanced. Even with the erect species, leaf longevity was promoted by growing the plants in humidity chambers.

In the greenhouse, flowering took place mostly from October through January. Many of these comparatively large grasses seemed to require about a year of vegetative growth before flowering commenced. However, several plants of *L. anomala* flowered less than six months from the date of germination.

Anatomical Studies

Collections were made both in the greenhouse and in the field. Greenhouse material was used for most part for comparative studies of cross-sectional leaf anatomy since those plants were grown under uniform conditions. Field collections were used only in a few cases when no greenhouse plants of the species were available. In each case, the first fully expanded blades of vegetative culms were sampled. This tended to insure that leaves of comparable age were used. However, this was probably not always strictly true since some plants were slow growing and others fast growing, the leaf samples of the former, therefore, being older.

Cross-sections of leaves about 0.5–1.0 cm wide were cut about ⅓ the distance from the base of the leaf blade. These sections were fixed in FAA (Sass, 1958). Dehydration was with tertiary-butanol and embedding was in Tissuemat (62°C mp). Sections were cut at 10–15 μm with "diSPo" disposable knives. Much tearing of tissues was experienced, probably due to the silica bodies in the epidermis. Soaking the embedded material for 24 hours in a softening solution (Pohl, 1965) alleviated the problem somewhat. Sections were stained with safranin-fast green and mounted in Piccolyte.

Epidermal features were studied from paradermally cut sections processed in the same manner as cross-sections. In addition, some observations were made from leaves cleared according to the method of Shobe & Lersten (1967) and stained with chlorozal black E according to the schedule given by Lersten & Pohl (1969).

CYTOLOGICAL STUDIES

Both meiotic and mitotic chromosomes were studied. For meiotic material collected in the field, young inflorescences were fixed and stored in Newcomer's (1953) solution. Anthers were dissected from the spikelets and squashed in propiocarmine stain. Observations were made from fresh preparations and were documented either by drawings made with the aid of a Zeiss drawing apparatus or photomicrographs. Subsequently, voucher slides were made permanent with the liquid-CO_2 method of Bowen (1956). Young inflorescences collected in the greenhouse were fixed with aspiration in either 3 ethanol:1 glacial acetic acid, or 6 ethanol:3 chloroform:1 glacial acetic acid. Results were similar for both fixatives. The fixed inflorescences were stored in the freezer compartment of a refrigerator in the fixative or in 70% ethanol. Storage in alcohol under low temperatures was helpful in reducing substantially the number of microsporocytes which burst during squashing. Better preparations were obtained from greenhouse-fixed material than from field-fixed material.

Observations on mitotic chromosomes were made from root tips of germinated caryopses or potted plants In both cases, the number of dividing figures was low. Root tips were pretreated either in cold water at 2–4°C for 24 hours or with a saturated solution of 8-hydroxyquinoline for 4 hours at 14°C in order to arrest dividing cells at metaphase and to shorten and spread the chromosomes. Fixation was in 3 ethanol:1 glacial acetic acid. Root tips were stained with the Feulgen reagent and then squashed. Further procedure was identical to that used in the meiotic studies.

MORPHOLOGICAL MEASUREMENTS

All spikelet, ligule, and leaf measurements were made on dried herbarium specimens. Since leaf blades in *Lasiacis* vary from rudiments to fully developed on almost every branch, only the largest blades on each herbarium specimen were measured. The minimum values reported for blade length and width, therefore, do not represent the absolute minimum values, but only the minimum values for the largest leaves found on herbarium specimens. Ligule lengths were measured on the two leaves immediately below an inflorescence. Spikelets were measured in side view from the middle of the pedicel to the tip of the spikelet. Inflorescence length was measured from the lowest node even though that node often has only rudimentary branches.

GROSS MORPHOLOGY

ROOTS

The root system among *Lasiacis* species is quite uniform and, except for the mode of root initiation, does not provide many characters of systematic importance.

Hoshikawa (1968, 1969) has made an extensive survey of the morphology of grass seedlings, emphasizing the mode of root initiation and seedling establishment. Six morphological types were recognized which correlated well with

the six subfamilies commonly recognized in modern systems of grass classification.

The following species of *Lasiacis* were examined, after germination under conditions similar to those detailed by Hoshikawa (1969): *L. anomala*, *L. divaricata*, *L. ligulata*, *L. linearis*, *L. oaxacensis*, *L. procerrima*, *L. rhizophora*, *L. ruscifolia*, *L. scabrior*, and *L. sorghoidea*. The radicle emerges first and produces the primary root. This primary root soon branches to produce secondary rootlets. In the terminology of Hoshikawa (1969), the seedlings may be described as follows: No roots are formed from the basal portion of the primary root (–), i.e., no "transitionary node roots" are formed. The mesocotyl elongates readily (+), and at least a few mesocotylar roots are formed consistently (+) (Fig. 1). In Hoshikawa's (1969) notation, *Lasiacis* is typified by the seedling formula –, +,+, In this notation, (–) indicates the absence of that character and (+) its presence. This formula is identical to that for all genera of the Paniceae that have been examined.

Several other features of the roots of mature plants may be noted. All species produce adventitious roots, especially at the lower nodes. Those of the erect species, except for *L. procerrima*, are similar and inconspicuous. *Lasiacis procerrima* usually produces large, prominent, adventitious prop roots from the lower nodes. Often the entire plant may be supported above the soil surface by these prop roots, which always remain unbranched until they reach the soil surface. Similar, but less conspicuous, roots are produced by the creeping species.

Upon bending, lodging, or falling to the ground, all erect species can produce adventitious roots at the culm nodes. When this happens, vegetative reproduction sometimes takes place.

CULMS

The culms or stems of many *Lasiacis* species are remarkable for their large size and woody appearance, and I refer to species possessing these as erect, woody species (Fig. 2). Culms are generally 1–5 m long, but I have observed one plant to reach 10 m in length. The woodiness is not due to secondary growth but to a large amount of lignified primary tissue. A cross-section of the culm shows a series of 2–8 rings of separate vascular bundles embedded in a parenchymous ground tissue. Beneath the epidermis is a layer of sclerenchyma fibers. This fibrous layer is relatively well developed in the woody species. Along with the lignification of some parenchyma of the ground tissue in maturing culms, the fibrous layer beneath the epidermis and the sclerenchyma fibers associated with the vascular bundles give the culm its mechanical strength.

Although the culms of the woody species can be generally described as erect, they are in fact often climbing or scandent, usually arching and supported in part by the surrounding vegetation. In many cases, the culms cannot support themselves, and if the surrounding vegetation is removed, the culms bend down to the ground. The ability to grow erect into the surrounding vegetation depends on the growth and branching habits of the culms. Buds from the lower nodes of existing culms produce vigorous young shoots which quickly elongate

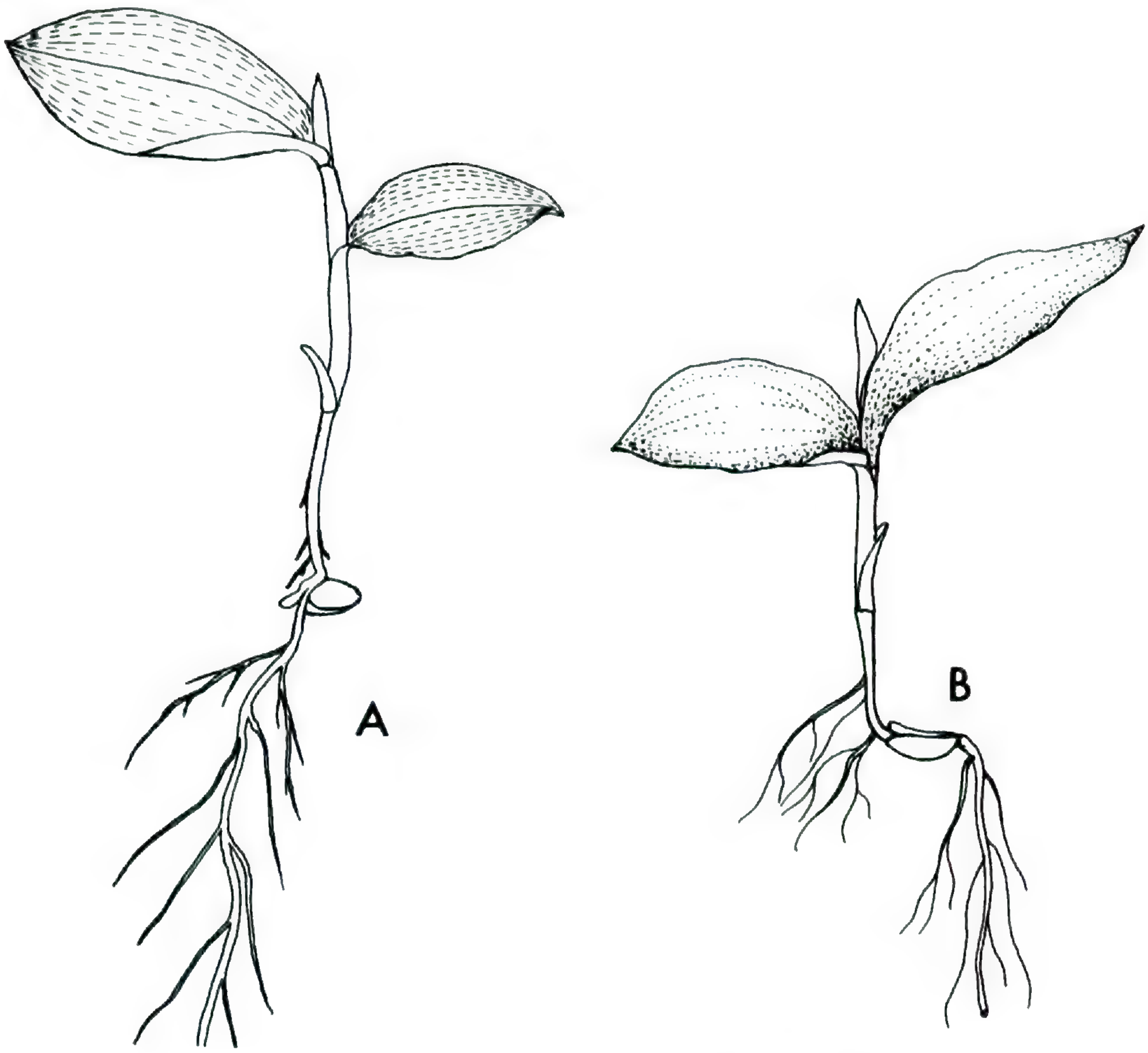


Figure 1. *Lasiacis* seedlings.—A. *L. nigra*.—B. *L. ruscifolia* var. *ruscifolia*.

without branching. When the new culm has reached its approximate maximum length, branching from the upper nodes is initiated. The initial growth in length can be supported in an erect or slightly arching position by the mechanical tissue of the culm. With increased branching, the weight of the culm becomes too great, and it will begin to bend down. However, since the initial growth of the main culm pushes it into surrounding vegetation, the culm can then be supported.

The creeping species have a culm anatomy similar to the erect species. The main difference is the smaller size and smaller amount of lignified tissue and the production of roots at nearly all nodes (Fig. 2).

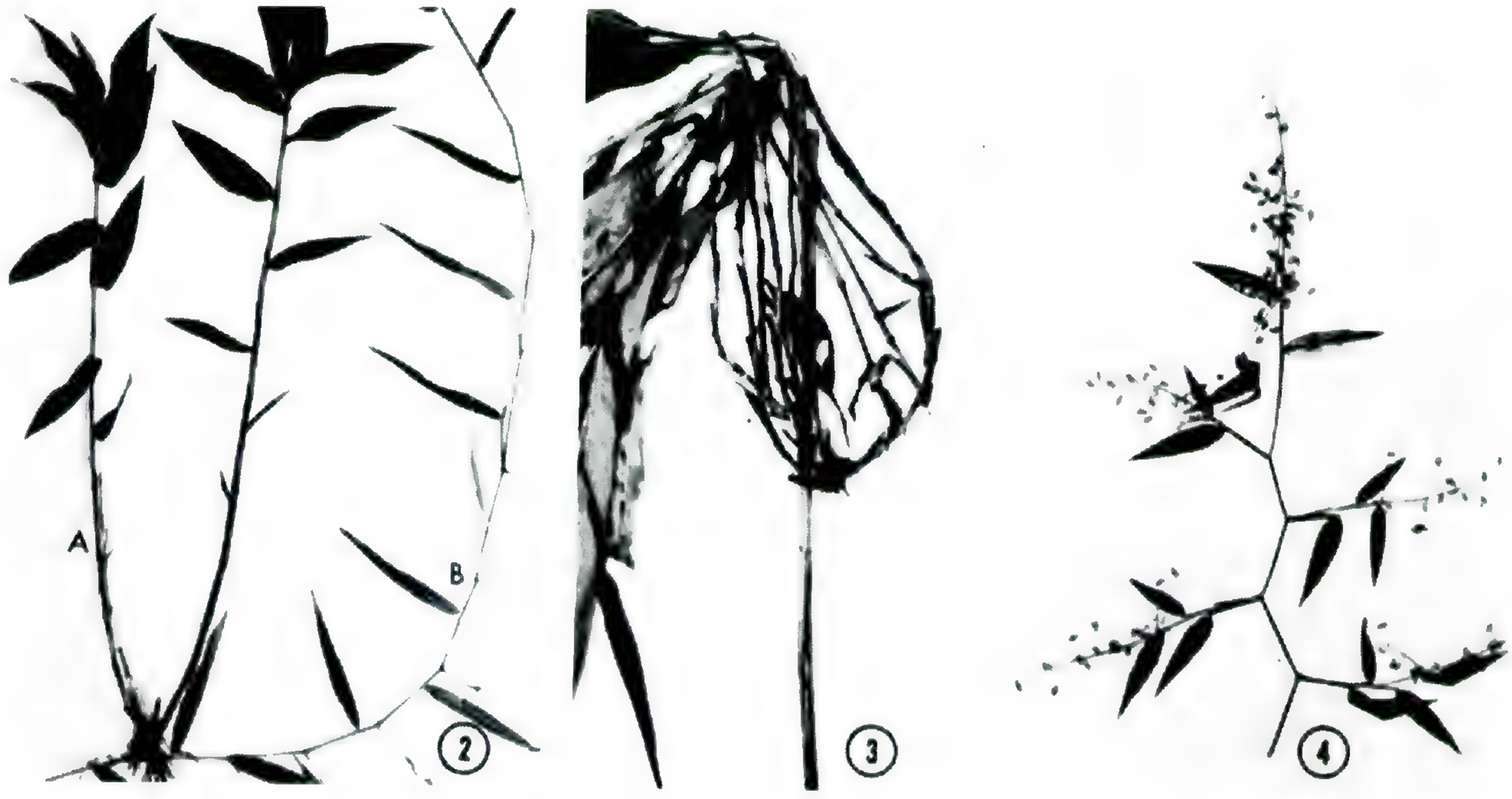
Culm Internodes.—Three of the creeping species, *L. linearis*, *L. oaxacensis*, and *L. rhizophora*, have solid, pithy internodes. Of the erect woody species, many specimens of *L. divaricata* var. *leptostachya* may have partially solid culms, and in *L. ruscifolia* var. *ruscifolia* there are a few local populations in Ecuador that have solid culms. The pith consists of thin-walled parenchyma cells, and it lacks vascular bundles, in contrast to the stems of most other monocotyledons and even some grasses such as *Zea mays*. The pith remains

almost indefinitely, although it may occasionally break down in old internodes of *L. linearis*. In the species with hollow internodes, the pith disappears early in the ontogeny of the culm. By the time a leaf has fully expanded, the pith remains only as an internal lining in the hollow internode above the base of the fully expanded leaf.

Although many standard reference works (e.g., Arber, 1934; Lawrence, 1951; Chase, 1959; Bor, 1960) state that grass internodes are usually hollow, Brown, Harris & Graham (1959) pointed out that this statement is misleading or incorrect when applied to the grass family as a whole. They demonstrated that 54% of a sample of 190 species had solid internodes. Solid internodes occur frequently in panicoid and chloridoid grasses but rarely in pooid grasses. In the tribe Paniceae, 49% of the species examined had solid internodes. In the light of these results, *Lasiacis* has an atypically low percentage of species with solid internodes.

Pulvini.—The ability of grass stems to straighten after becoming lodged is in a large part due to pulvini which can be recognized as swellings at the base of an internode. Differential growth in the pulvini results in the upward bending of culms. Pulvini, depending on their location, are called sheath pulvini or culm pulvini (Hackel, 1890; Arber, 1934; Brown, Pratt & Mobley, 1959). In all *Lasiacis* species, the culm pulvinus is prominent and strongly developed. A slight thickening at the base of the sheaths indicates that there is a poorly differentiated sheath pulvinus. This pulvinus is evident in very young leaves before a culm pulvinus is clearly differentiated. It is likely, therefore, that the sheath pulvinus is active in early growth, the function being carried on subsequently by the culm pulvinus in older parts of the culm. In the possession of culm pulvini, *Lasiacis* is typical of the Panicoideae. The Pooideae, in contrast, rarely have culm pulvini (Brown, Pratt & Mobley, 1959).

Branching patterns.—Most mature *Lasiacis* plants are highly branched. Branching in all species is intravaginal, the new branches emerging between the culm and the subtending sheath. Rare exceptions to intravaginal branching have been observed in *L. procerrima*. Branches develop from buds at the nodes. Those branches that develop from buds on the main culm I call primary branches. The next order of branching is referred to as secondary branching and so on. Only one primary branch forms at each node of the main culm. Subsequent modes of branching may result in quite different plant bodies. In one type of branching, the primary branch may produce a number of secondary branches. The next order of branching is referred to as secondary branching primary one in length. Since the lowest internodes of a branch are very short, this results in a fascicle of branches (Fig. 3). A second type may be called an open one since it characteristically produces well-spaced secondary and tertiary branches throughout the length of the primary branch (Fig. 4). The two types of branching grade into each other. Fascicled branching occurs most frequently at the upper nodes of large culms, while the open form is most characteristic of the lower nodes. In mature plants it is also common to see fascicles of secondary and tertiary branches at the upper nodes of a primary branch. Fascicled branch-



FIGURES 2–4. Gross morphology of *Lasiacis*.—2. Comparison of growth habit.—2A. *L. ruscifolia* var. *ruscifolia*, an erect woody species; note rudimentary blades at the lower nodes.—2B. *L. oaxacensis* var. *maxonii*, a creeping, herbaceous species, rooting at the nodes.—3. Fascicled branching in *L. sorghoidea* var. *sorghoidea*.—4. Open branching and zigzag culm in *L. rugelii* var. *rugelii*.

ing does not occur in the creeping species. These species always produce one branch per node, and the size distinction between the main culm and its branches is usually soon lost.

Branching pattern is of limited diagnostic value in *Lasiacis*. However, it characterizes *L. divaricata* var. *divaricata* and *L. rugelii* var. *rugelii*. In both varieties, the upper main culms become zigzag after branching (Fig. 4). The main culm is initially straight, but as the primary branch begins to grow, the main culm diverges in the opposite direction. Since leaf arrangement is alternate, the end result is a zigzag pattern. The divergence of the main culm seems to be caused by differential growth of the culm pulvini. The divergence of the primary branch is frequently so great that this branch becomes reflexed, thus forming a hooklike structure which is effective as a climbing device. It also aids in maintaining support for the main culm. A similar zigzag pattern may develop on vigorous primary branches when they produce secondary branches.

LEAVES

Avdulov (1931) pointed out the importance of the shape and position of the first seedling leaf in the systematics of the Gramineae. He recognized two types. The first, which corresponds to the pooid type, has a linear, perpendicular first leaf. The other, the panicoid type, has an oval, lanceolate, or oblong, horizontal, or ascending first leaf. Stebbins (1956) and Stebbins & Crampton (1961) subsequently stressed the importance of seedling leaves. Kuwabara (1960) made detailed observations on a number of species and found his observations, with several exceptions, to agree closely with those of Avdulov. The first leaves in seedlings of *Lasiacis* species are relatively broad, and their position

is horizontal to slightly ascending above the soil surface (Fig. 1). Of the species examined, *L. linearis* and *L. oaxacensis* have linear-lanceolate first leaves, thus reflecting the shape of the mature leaves. The remaining species, *L. anomala*, *L. divaricata*, *L. ligulata*, *L. rhizophora*, *L. ruscifolia*, *L. scabrior*, *L. sloanei*, and *L. sorghoidea*, have broadly elliptic or oval leaf blades. In seedling leaf morphology, *Lasiacis* is typically panicoid.

Lasiacis is similar to many other tall grasses such as *Olyra*, *Phragmites*, and bamboos in that the lowest leaves on new culms are nearly bladeless (Fig. 2). Higher up the culms, the blades become increasingly developed.

The prophyll has not been examined in detail. This prominently 2-keeled structure varies in pubescence. In some species, such as *L. divaricata* and *L. rugelii*, which often have widely diverging branches, the prophylls may be prominently displayed. In other species, they are often hidden within the sheath of the subtending leaf.

Sheath margins are free, and the upper or overlapping margin is usually ciliate. The apex of the sheath occasionally extends as a narrow auricle beyond the apex of the sheath. This is most highly developed in *L. procerrima*. The collar, the abaxial surface of the junction of the blade and the sheath, has been called a petiole (Nuñez, 1952; Hsu, 1965) when elongated somewhat. More properly called a pseudopetiole, it is most highly developed in *L. sloanei* and rarely exceeds 3 mm.

INFLORESCENCE AND SPIKELETS

The inflorescence of all species of *Lasiacis* is a panicle. It provides many important diagnostic characters including size, mode of branching, and arrangement of the spikelets.

The spikelets of all *Lasiacis* species except *L. anomala* are of the *Panicum* type. They consist of two glumes and two florets arranged alternately and distichously on the common axis, the rachilla. The lower or sterile floret consists of a lower or sterile lemma, a palea, and sometimes a staminate flower of three stamens and two lodicules. Sterile is not used in the absolute sense but in the sense of Hitchcock (1951), who defines sterile to mean without a pistil. In many species, the sterile floret does not contain a flower at all or contains only the rudiments of one. The upper or fertile floret consists of an upper or fertile lemma, a palea, and the included, perfect flower which is composed of two lodicules, three stamens, and a pistil with two free styles and stigmatic branches. At maturity, the fertile floret becomes indurate whereas the other bracts retain their soft texture. *Lasiacis* is unique in developing a shiny black color in the glumes and sterile lemmas after the caryopsis has fully matured. This seems to be an adaptation for bird dispersal (Davidse & Morton, 1973).

The spikelet of *L. anomala* is basically the same as the *Panicum* type but differs in bearing one additional bract, called a sterile lemma by Hitchcock (1919). Therefore, the spikelet of *L. anomala* bears two glumes, two sterile florets, and one fertile floret. The extra sterile lemma never encloses a palea, and for this reason, the extra bract could with equal justification be called an extra

glume. The presence of such an extra bract occurs only rarely in the Paniceae, another example being *Panicum quadriglume* (Doell) Hitchc. from South America.

DEVELOPMENTAL MORPHOLOGICAL VARIATION

A considerable amount of developmental morphological variability is exhibited by *Lasiacis* species. This variation is most conspicuous in the development of leaves, inflorescences, and pubescence. I have already noted that the culms in all species tend to be highly branched. With each successive order of branching, leaves become smaller, so that it is not unusual for fully expanded leaves on secondary branches to be one-third the size of those on the main culm. There is also often a reduction in the size of the inflorescences on secondary branches. There are two notable developmental variation patterns in pubescence. It is quite common for leaves of secondary and tertiary branches to be conspicuously more densely pubescent than primary leaves. This phenomenon is also common in new, young, vigorous main shoots in large plants. The increased pubescence is especially prominent in both cases on the lower leaves of the branch or shoot. On fully mature main culms, the younger leaves may often become glabrate in comparison to the lower ones.

Recognition of such developmental variation becomes quite important in such large plants as those of *Lasiacis* since specimens are often fragmentary. Care must, therefore, be exercised in relating variation observed among specimens to the causative agent which may be developmental, environmental, or genetic.

DURATION

All species of *Lasiacis* are perennial, or at least potentially so. According to Hitchcock (1920), *L. procerrima* is annual. This may be true in certain habitats, especially disturbed, bare roadsides or similar extreme ecological niches in which *L. procerrima* often becomes very depauperate. In regions with a definite dry season, such plants probably rarely survive more than one growing season. In more stable secondary communities with more favorable moisture conditions, I have observed large, branched plants in which the terminal portions of the culm bore old inflorescences. The lower parts of the main culms were still producing new branches with new inflorescences. This indicates survival through at least two growing seasons. In the greenhouse, *L. procerrima* also acts as a perennial.

There is also a question whether the individual culms of the erect, woody species are perennial. Dr. Paul Weatherwax (pers. comm.) has indicated that he believes *Lasiacis* to be a herbaceous perennial since the aerial parts die down to the ground after flowering, new shoots coming up later from the underground parts. This is invariably true of the small "seedling" culms that produce inflorescences. After larger culms have been formed, the strictly vegetative "seedling" culms often undergo the same fate. However, in well-developed culms, several courses may be followed. If primary branches have been formed and the main

culm produces a terminal inflorescence, the primary branches may remain vegetative and flower the next year. Such a culm is perennial. If both the main culm and the primary branches produce inflorescences, the culm does not necessarily die, but it may produce new branches, usually in fascicles which later can produce new inflorescences. Such fascicled culms, even in their natural habitat, no doubt take two years to grow to maturity.

Leaf Anatomy

The importance of leaf anatomy in providing characters for use in classification was already recognized in the 19th century by Duval-Jouve (1875) on the basis of his studies of several different cell types in various grass species. Avdulov (1931) recognized two major groups on the basis of leaf anatomy. These two groups corresponded to his two major subdivisions of the Gramineae, the Poatae and the Sacchariferae. In modern terminology, these groups are referred to as pooid and panicoid, respectively. Prat (1932, 1936) in two classic papers pointed out the importance of the epidermis as a source of taxonomic characters. He used these, plus other characters, to propose three subfamilies: Festucoideae, Bambusoideae, and Panicoideae (Prat, 1936). Numerous recent contributions have shown the usefulness of leaf anatomy in grass systematics. Several of general interest and importance may be noted. Brown (1958), placing emphasis on the presence or absence of bundle sheaths and the arrangement of the chlorenchyma, recognized six anatomical groups. Five of these correspond closely with the subfamilies now generally recognized. Metcalfe's (1960) monumental work brought together original and published diagnostic specific and generic descriptions based on characters of the epidermis and transverse section of the blade. In his discussion, three major anatomical groups were recognized, corresponding to the pooid, panicoid, and bambusoid grasses. Several subgroups of the panicoid type were also described. Tateoka et al. (1959) surveyed 238 species of grasses and found that, with few exceptions, the Eragrostoideae, Panicoideae, and Bambusoideae have distinctive types of bicellular hairs.

In recent years many of the anatomical characters which have proven useful in the classification of grasses have been linked to physiological characters associated with two systems of photosynthesis, the C_3 and C_4 systems (Hatch & Slack, 1970; Carolin & Jacobs, 1973; Johnson & Brown, 1973; Smith & Brown, 1973; Laetsch, 1974; Brown, 1975). Plants with C_4 photosynthesis fix carbon initially into 4-carbon compounds and those with C_3 photosynthesis into 3-carbon compounds. Other physiological and biochemical characters associated with C_4 plants, as compared to C_3 plants, are low CO_2 compensation points, high rates of net photosynthesis, higher optimum temperatures for photosynthesis, reduced photorespiration, and greater compartmentalization of biochemical reactions. C_4 plants have a distinctive anatomy, called a Kranz anatomy, characterized by a prominent parenchyma bundle sheath around each vascular bundle. The cells of this bundle sheath are large, thick-walled, possess specialized chloroplasts, store starch, and have a dense cytoplasm. The mesophyll tends to be highly radial around the vascular bundles and does not accumulate starch. In C_3 plants with a non-Kranz anatomy the cells of the parenchyma bundle sheath have few

or no unspecialized chloroplast, do not accumulate starch, and usually have large vacuoles and little cytoplasm. The mesophyll is not strictly radially arranged and stores starch. One of the important consequences of these correlations is that it is now possible to hypothesize in functional terms about the possible adaptive nature of these sets of characters, although it is often difficult to place these hypotheses in a phylogenetic context for specific genera and species.

Except for a brief characterization of the parenchyma sheath of *L. procerrima* by Carolin & Jacobs (1973), no studies of leaf anatomy have been reported for *Lasiacis*. However, without providing any published data, Nuñez (1952) stated that: "La estructura histofoliar [of *Lasiacis*] revela semejanzas con la de géneros pertenecientes a la subfamilia *Bambusoideae* Roshevitz." Hsu (1965) conducted an extensive survey of *Panicum* species and representative species of other genera of the Paniceae using characters of the lodicules, style bases, and epidermal patterns of the lemmas. In his discussion of *Lasiacis*, Hsu (1965) stated that: "The anatomical leaf structure of this genus is similar to bamboos." Again no data or illustrations were provided.

Since both Nuñez (1952) and Hsu (1965) suggested that leaf anatomy might be of the bambusoid type or closely related to it, I have investigated leaf anatomy as seen in cross-sections of the blades and surveyed the blade epidermis in seven representative species. The terminology employed throughout the discussion of leaf anatomy follows that of Metcalfe (1960).

LEAF BLADE IN CROSS-SECTION

General Characteristics.—Unless otherwise stated, the general description that follows applies to all species examined. A complete list of the vouchers for the species examined anatomically is given in Table 1.

All species contain three clearly differentiated types of vascular bundles (Fig. 5). The first of these, the main vascular bundle (MVB), is the largest vascular bundle in the leaf and is contained in the midrib of the blade (Figs. 10, 12). The clearly differentiated xylem and phloem of the MVB is surrounded by an inner bundle sheath (IS) of sclerenchyma fibers. It is also surrounded by a single- or multi-layered parenchyma bundle sheath or outer bundle sheath (OS). Inside the adaxial and abaxial epidermis and above and below the MVB are two girders of sclerenchyma fibers. The OS may be interrupted adaxially and/or abaxially by an extension of sclerenchyma which connects the sclerenchyma of the IS with that of the sclerenchyma girders. The combined cross-sectional appearance of the sclerenchyma girders of the MVB is always anchor-shaped, i.e., the adaxial girder is narrow and the abaxial girder is very broad (Fig. 5). The vascular bundles of the lamina of the blade may be distinguished as primary vascular bundles (PVBs) and secondary vascular bundles (SVBs). The PVBs are separated from each other by 3–7 SVBs (Fig. 5). The PVBs are large and the xylem and phloem is clearly differentiated (Figs. 6, 8). In addition, the PVB has one prominent metaxylem vessel element to each side of the protoxylem, has a well-developed IS and OS, and is accompanied by abaxial and adaxial sclerenchyma girders. The SVBs are small, angled, and the xylem and

TABLE 1. Voucher specimens examined for leaf anatomy. The plants were grown from seed collected in the indicated localities.

L. anomala

TRINIDAD: Between Piarco and Piarco Int. Airport, *D 2522*,[a] *D 2523*; Irois Bay, *D 2580*;[a] 2 mi post, Mausiga Rd., NE of Piarco, *D 2591*.[a]

L. divaricata var. *divaricata*

UNITED STATES: Florida: Monroe Co., 10 mi NE of Flamingo, *Deam s.n.* HONDURAS: Atlantida: 17 km SSE of La Ceiba, *DP 2196*. Comayagua: San José de Comayagua, *DP 2226*. NICARAGUA: Zelaya: Río Coco at Bilwaskarma, *DP 2295*. DOMINICAN REPUBLIC: La Vega: 18 km N of Jarabacoa, *D 2633*.

L. ligulata

TRINIDAD: 6 mi N of Port-of-Spain along North Coast Rd., *D 2561*; Between La Vache and Maracas Bay, *D 2566*.

L. linearis

HONDURAS: Morazán: Mt. Uyuca, *DP 2100*.

L. nigra

HONDURAS: El Paraíso: 7 km NW of San Lucas, *PD 12161*.

L. oaxacensis var. *oaxacensis*

EL SALVADOR: Libertad: Volcán de San Salvador, *DP 2026*. MEXICO: Tabasco: 9 mi NW of Santiago Tuxtla, *PD 11818*.

L. oaxacensis var. *maxonii*

HONDURAS: Yoro: 15 km SSE of Río Viejo, Rd. to Olanchito, *DP 2199*.

L. procerrima

HONDURAS: Morazán: 8 km E of El Zamorano, *DP 2081*. COLOMBIA: Caquetá: Florencia, *Soderstrom s.n.*

L. rhizophora

HONDURAS: Morazán: Mt. Uyuca, *P 12489*. COSTA RICA: San José: S of Curridabat, *PD 11694*.

L. ruscifolia var. *ruscifolia*

MEXICO: San Luis Potosí: Near Xolol, *PD 11808*. EL SALVADOR: Libertad: 1.5 km E of Apulo, Lago Ilopango, *DP 2033*. HONDURAS: Cortes: 1 km S of Puerto Cortes, *DP 2169*. Atlantida: 9 km E of Tela, *DP 2188*; 17 km SSE of La Ceiba, *DP 2198*. COSTA RICA: Guanacaste: Vicinity of Cañas, *Daubenmire 169*; Puerto Castillo, *PD 11562*.

L. ruscifolia var. *velutina*

HONDURAS: Morazán: Between El Zamorano and San Antonio de Oriente, *DP 2162*, *P 12508*.[a]

L. scabrior

HONDURAS: Atlantida: 28 km NE of El Progreso, *DP 2173*.

L. sloanei

HONDURAS: Yoro: 19 km SE of Río Viejo, *DP 2200*. COSTA RICA: Limón: Near Pandora, *PD 11123*.

L. sorghoidea var. *sorghoidea*

COSTA RICA: Puntarenas: Near San Vito de Java, *PD 10790*. TRINIDAD: Northern Range, near Heights of Guanapo, *D 2460*.

[a] Both field collections and greenhouse plants examined.

FIGURE 5. Cross-section of leaf blade of *Lasiacis ruscifolia* var. *ruscifolia*; note the main (mvb), primary (pvb), and secondary (svb) vascular bundles.

phloem are not as clearly differentiated as in the PVBs, although these tissues are usually recognizable (Figs. 7, 9, 14). The SVBs also lack the IS and prominent metaxylem elements. The OS is, however, usually more prominent than in the PVBs. Small adaxial and abaxial girders usually accompany the SVBs.

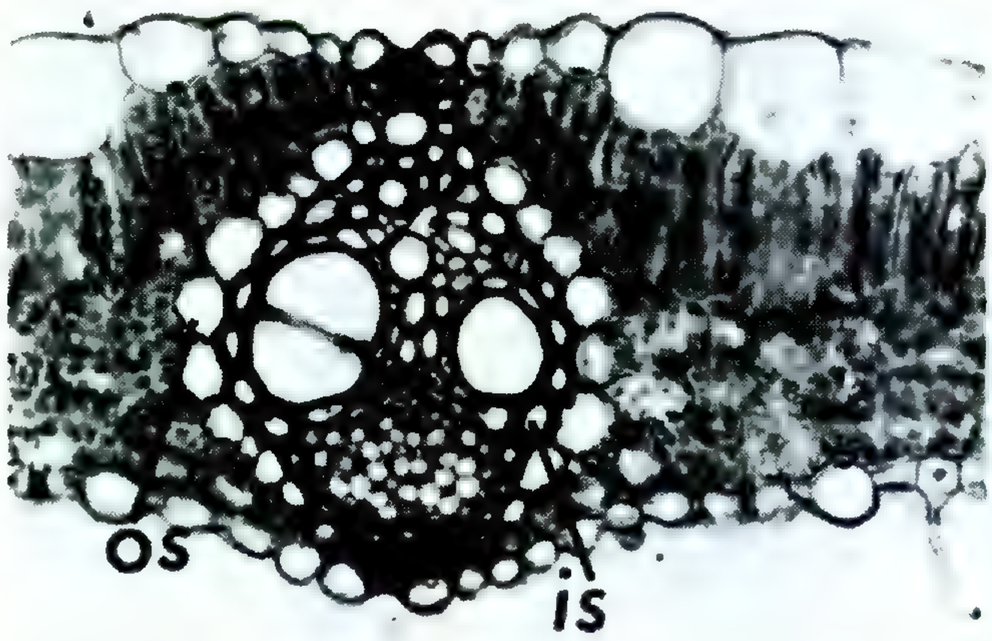
The arrangement of the chlorenchyma is very characteristic and similar in all species. Palisade and spongy layers are differentiated (Figs. 6–7). The palisade layer is made up of a single layer of elongated chlorenchyma cells. The spongy tissue is made up of cells that are usually irregularly spherical or somewhat elongated. A single layer of elongated chlorenchyma cells is arranged radially around the PVBs and SVBs (Figs. 9–14).

Bulliform cells occur in the adaxial epidermis; they are sometimes quite large, well differentiated, and arranged in regular groups (*Zea* type; Metcalfe, 1960; Figs. 11, 13). In most species, the cells are not as large and conspicuous as in the *Zea* type. Ribs and grooves are inconspicuous in all species, although they are present to a slight extent next to the midrib, especially on the adaxial surface.

Starch is absent in the outer parenchyma sheath of all species but accumulates in the chlorenchyma of the palisade and spongy layers.

Characteristics of Individual Species.—Characteristics of the cross-sectional leaf anatomy for each species are presented in Tables 2 and 3. For consistency, all observations were made on the set of PVBs and SVBs immediately adjacent to each side of the MVB. Some changes in the configuration of the tissues and size of cells takes place toward the margin of the blade: bulliform cells usually become smaller and less conspicuous, the PVBs become smaller, and adaxial extensions of the OS of the SVBs become smaller or disappear.

Leaf blades of most *Lasiacis* species are similar anatomically. *Lasiacis procerrima*, in parallel with its gross morphological distinctiveness, is anatomically very distinct. It has thick leaves, well-developed bulliform cells, multilayered bundle sheaths, large sclerenchyma girders, and MVBs with two closely associated SVBs (Fig. 10). *Lasiacis oaxacensis* is most similar anatomically to *L. procerrima* (Fig. 12). It also has two SVBs closely associated with the MVB.



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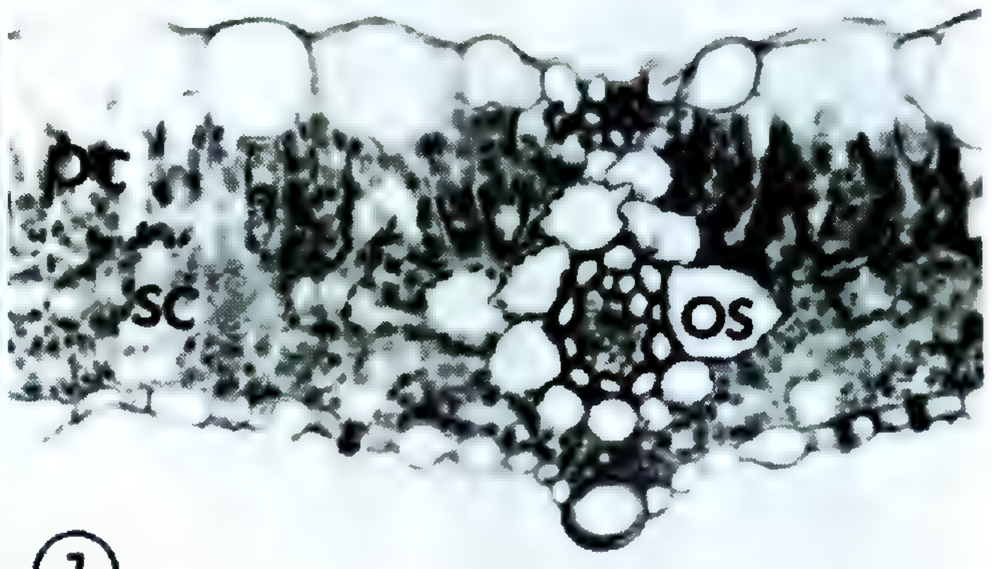

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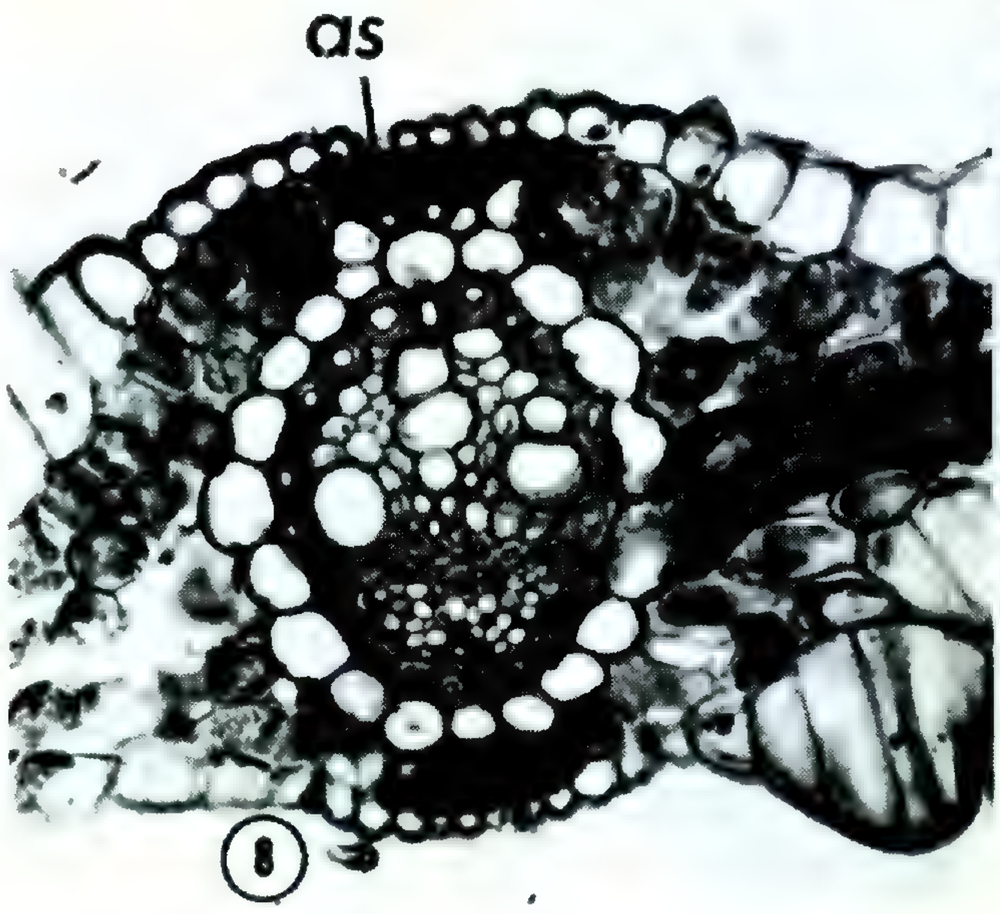

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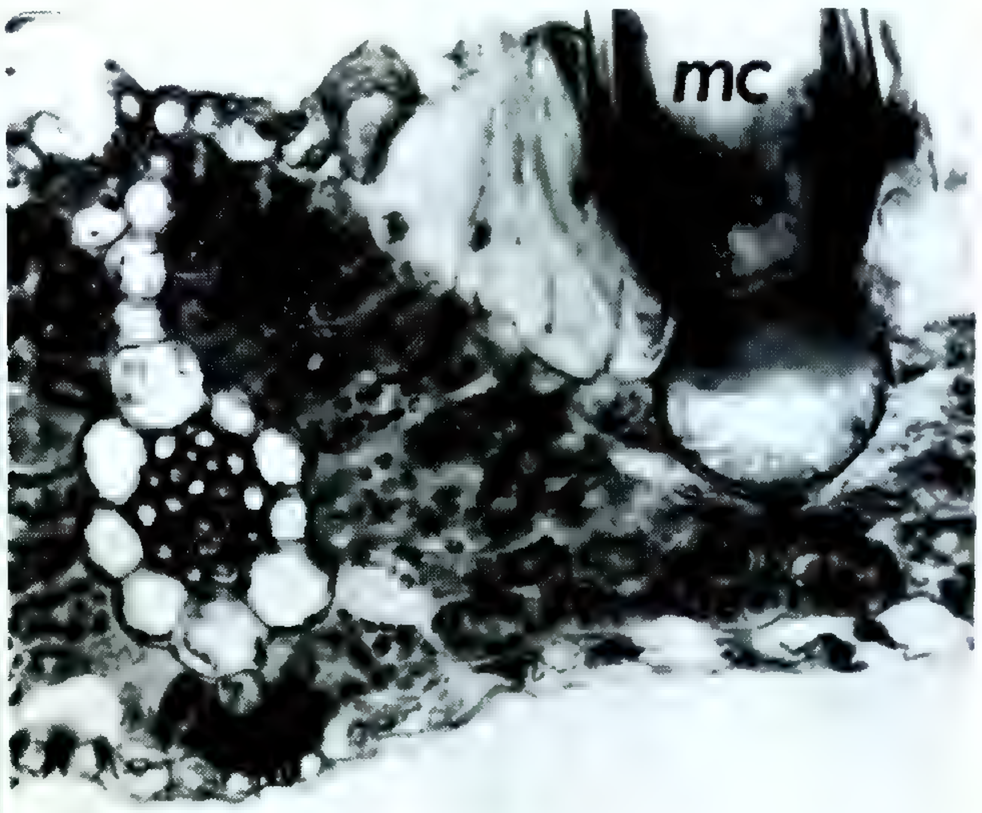

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FIGURES 6–9. Cross-section of leaf blades of *Lasiacis* species.—6. Primary vascular bundle of *L. anomala*; note the interrupted outer sheath.—7. Secondary vascular bundle of *L. anomala*.—8. Primary vascular bundle of *L. rhizophora*; note the continuous outer bundle sheath.—9. Secondary vascular bundle of *L. rhizophora*; note sunken base of macrohair. Abbreviations: as = adaxial sclerenchyma strand; is = inner bundle sheath; mc = macrohair; os = outer bundle sheath; pc = palisade chlorenchyma; sc = spongy chlorenchyma.

In all other species, SVBs may occasionally diverge from the MVB and in the appropriate cross-sections thus appear closely associated with the MVB. In these species, the association is not consistent throughout the length of the blade.

In *L. ruscifolia* and *L. anomala*, the OS of the PVBs is interrupted (Fig. 6). In all other species, the OS of the PVB is usually complete, but an interruption can be observed infrequently, in which case it is probably due to the lignification of the outer bundle sheath cells between the IS and the schlerenchyma girders.

One curious and anomalous observation was the presence of arm cells in the chlorenchyma of a single field collection (*D 2580*) of *L. anomala*. Examination of greenhouse progeny from the same plant sampled for the field collection failed to demonstrate these cells. Neither were they noted in field collections and greenhouse collections of *D 2522* and *D 2591*, both also collections of *L. anomala*. Arm cells are characteristically present in the chlorenchyma of bam-

TABLE 2. Anatomical character states for *Lasiacis* leaf blade cross-sections (adapted from Metcalfe, 1960).

Sclerenchyma	
1.	PVB with small adaxial and abaxial girders.
2.	PVB with low, wide, somewhat triangular adaxial and abaxial girders.
3.	PVB with combined adaxial and abaxial girders anchor-shaped.
Midrib	
4.	MVB single or occasionally with one or two closely associated SVBs.
5.	MVB always with two closely associated SVBs.
Bulliform Cells	
6.	Bulliform cells conspicuously large, in regular group—*Zea* type.
7.	Bulliform cells in well-defined, regular groups but only gradually larger than the remaining epidermal cells.
Chlorenchyma	
8.	Chlorenchyma of spongy layer conspicuously elongated and arranged perpendicularly to the palisade chlorenchyma.
9.	Chlorenchyma with arm cells.
10.	Chlorenchyma not conspicuously elongated or with arm cells.
Bundle Sheaths	
11.	IS and OS of PVB complete, sometimes with slight adaxial extension of colorless cells.
12.	IS and OS of PVB complete, IS two or three cells wide below the phloem, OS variously multilayered.
13.	IS of PVB complete; OS interrupted adaxially and abaxially.
14.	IS of PVB complete; OS interrupted abaxially.
15.	IS of PVB complete; OS interrupted adaxially.
16.	OS of SVB with an adaxial extension of colorless cells.
17.	OS of SVB with adaxial and abaxial extensions of colorless cells.

busoid grasses. The significance of these cells in a single *Lasiacis* collection is not known.

Leaf anatomy generally is not useful for specific identification since the overlap in anatomical chacteristics between different populations of the same species and different species is too great; however, at least *L. procerrima* and *L. oaxacensis* can be reliably identified on this basis. Türpe (1966) in a study of Argentinian species of *Paspalum*, on the other hand, was able to show the existence of many specific differences. However, she noted that leaf anatomy could better be correlated with the ecological habitats of the plants than their taxonomic position within the genus. Since the species of *Lasiacis* are not diverse ecologically, there may be a corresponding lack in anatomical distinctiveness.

LEAF BLADE EPIDERMIS

The epidermal cells of grass leaves are arranged in rows parallel to the long axis of the blade. The zone of cells over the veins, the costal zone, is usually conspicuously different in appearance from the zone between the veins, the intercostal zone (Figs. 16, 19–20). The epidermis of grass leaves contains a number of distinct cell types which in *Lasiacis* include long cells, short cells (both cork and silica cells), guard cells and associated subsidiary cells, microhairs, prickle hairs, and macrohairs.

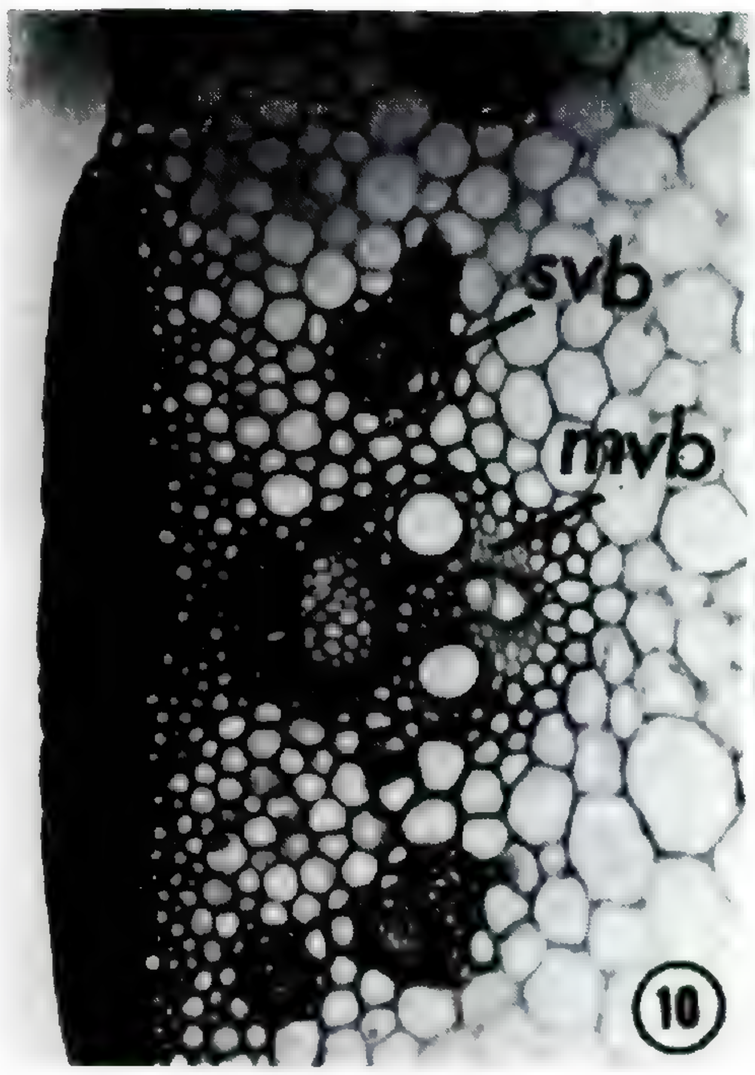
TABLE 3. Anatomical characteristics of *Lasiacis* species as seen in cross-sections of leaf blades.[a]

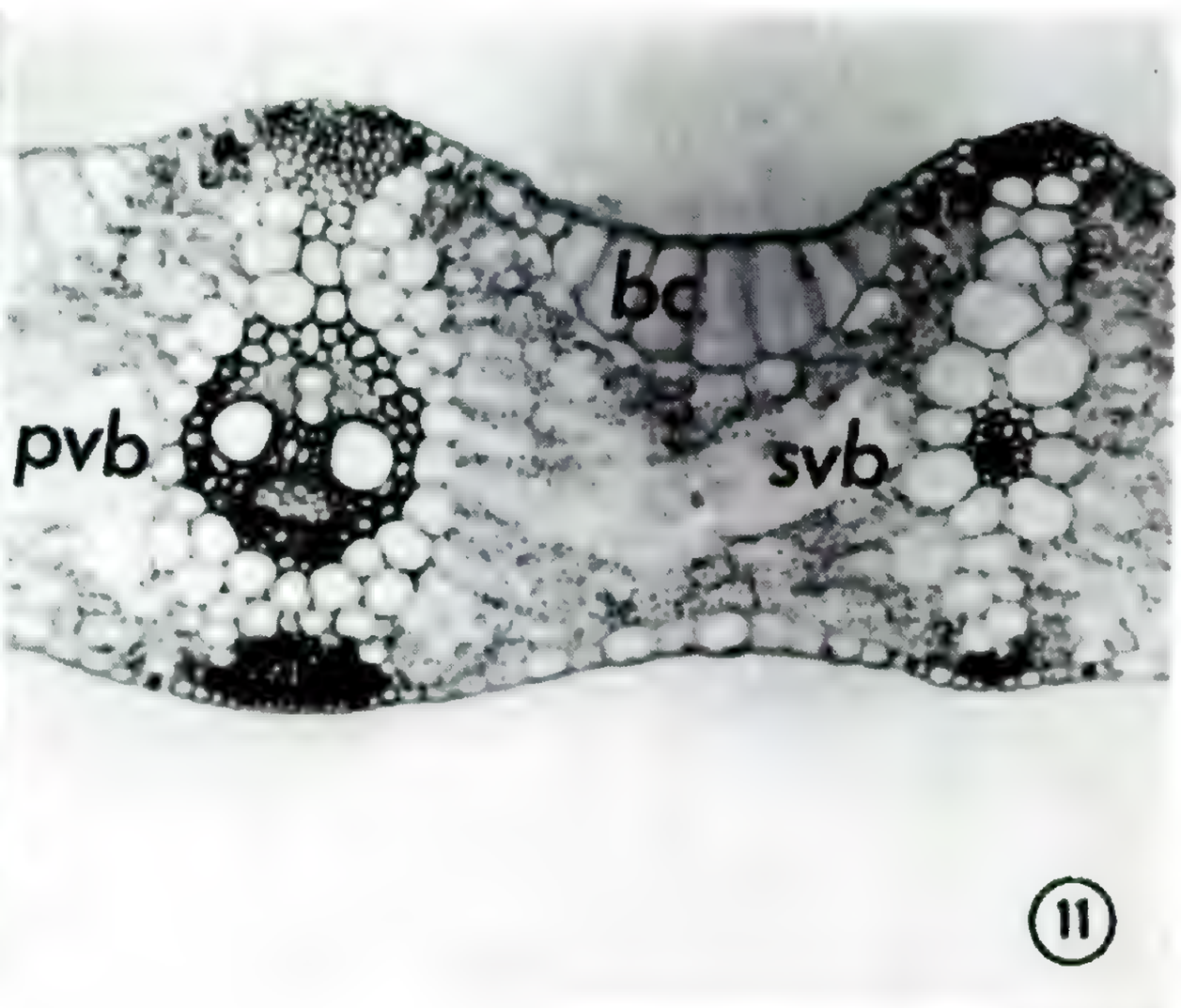
Species	Sclerenchyma	Midrib	Bulliform Cells	Chlorenchyma	Bundle Sheaths	
					PVB	SVB
L. anomala	1, 3[b]	4	7	9, 10	13, 14	16
L. divaricata var. *divaricata*	3	4	7	10	11, 14	16
L. ligulata	3	4	7	10	14	16
L. linearis	2-3[c]	4	7	10	11	16
L. nigra	1	4	7	10	11	16
L. oaxacensis var. *oaxacensis*	1-2	5	6	8, 10	11-13	16-17
L. oaxacensis var. *maxonii*	1-3	5	6	10	11	16
L. procerrima	2	5	6	8	12	17
L. rhizophora	1	4	7	10	11	16
L. ruscifolia var. *ruscifolia*	3	4	7	10	13, 14, 15	16
L. ruscifolia var. *velutina*	1-2	4	7	8, 10	11	16
L. scabrior	1	4	7	10	11	16
L. sloanei	3	4	7	10	11, 14	16
L. sorghoidea var. *sorghoidea*	3	4	7	10	11, 14	16

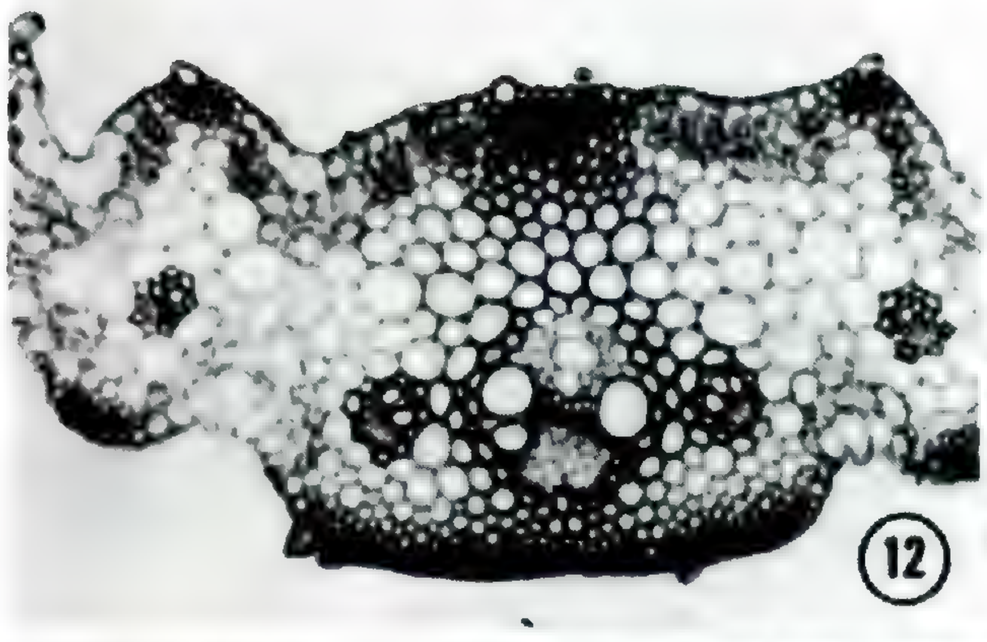
[a] Numbers in the table refer to the character states listed in Table 2.
[b] Numbers separated by a comma indicate that both character states have been observed in the taxon.
[c] Numbers connected with a hyphen indicate that an intermediate condition between the two indicated character states exist in the taxon.

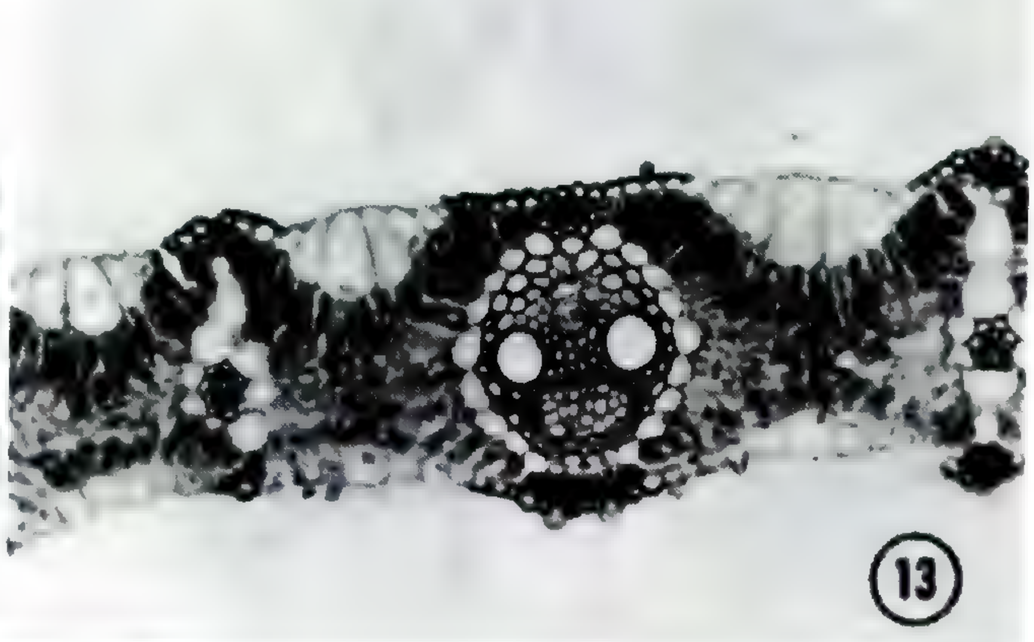
The following seven species have been examined for epidermal anatomy: *L. divaricata, D 2196*; *L. linearis, DP 2100*; *L. procerrima, Soderstrom s.n.*; *L. rhizophora, P 12489*; *L. scabrior, PD 11692*; *L. sloanei, DP 2200*; and *L. sorghoidea, PD 10790*. The following observations refer primarily to the adaxial epidermis, although the abaxial surface is quite similar. Long cells in the costal zones are relatively long and narrow with sinuous walls. Those of the intercostal zone vary, depending on the species, but are always larger than those of the costal zones. They may be nearly cubical or distinctly rectangular and possess sinuous or nearly straight cell walls. Between the costal and intercostal zones and associated with the PVBs is an intermediate zone of long cells in which the cells are like those of the costal zone but become wider and shorter toward the intercostal zone (Fig. 20).

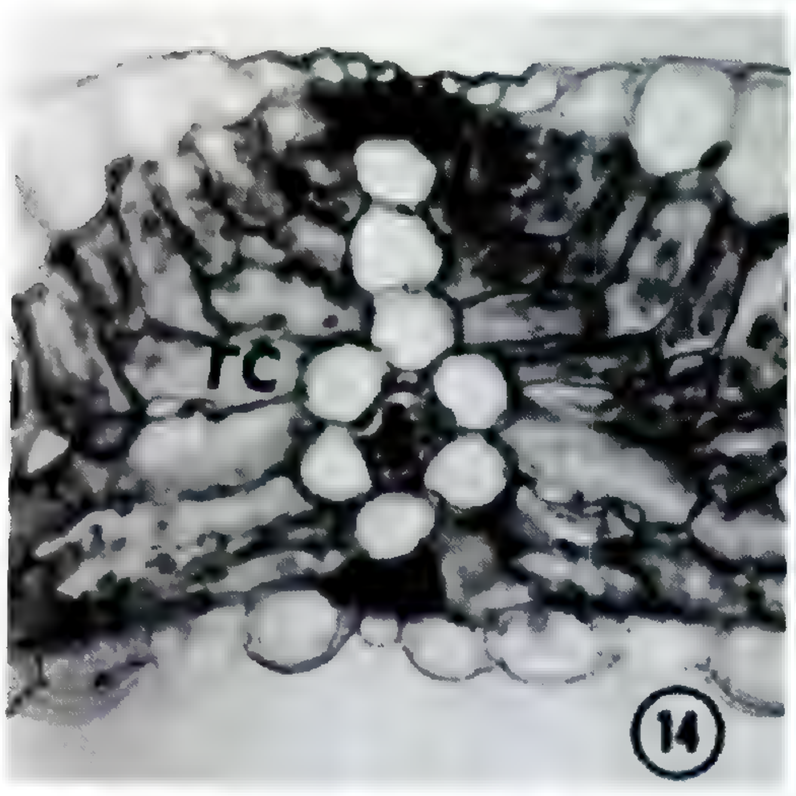
The short cells in the costal zones are arranged in long continuous rows, commonly with alternating silica and cork cells. The silica bodies within the silica cells are primarily dumbell shaped with a smaller number being nodular shaped (Figs. 17–20). No short cells occur in the intercostal zone. In the intermediate zone, short cells occur in pairs or occasionally singly, rather than in long rows as in the costal zone.











FIGURES 10–15.—10–14. Cross-sections of leaf blades of *Lasiacis* species.—10. Abaxial portion of the midrib of *L. procerrima*; note three secondary vascular bundles associated with the main vascular bundle.—11. Primary and secondary vascular bundles of *L. procerrima*.—12. Midrib of *L. oaxacensis* var. *oaxacensis*; note two secondary vascular bundles associated with the main vascular bundles.—13. Primary and secondary vascular bundle of *L. oaxacensis* var. *oaxacensis*.—14. Secondary vascular bundle of *L. rugelii* var. *pohlii*.—15. Biocellular microhair of *L. nigra*. Abbreviations: bc = bulliform cells; mvb = main vascular bundle; pvb = primary vascular bundle; rc = radial chlorenchyma; svb = secondary vascular bundle.

Stomata occur in one or two rows among the long cells on each side of the costal zone (Figs. 16, 19). The stomatal complex is made up of two dumbbell-shaped guard cells and two subsidiary cells. The shape of the subsidiary cells is typically triangular to low dome shaped (Figs. 16, 19).

Microhairs are bicellular (Fig. 15). The distal cells have much thinner cell walls than those of the basal cell and for this reason are often distorted. When undamaged, they can be observed to taper to a somewhat rounded point. In all but one of the six species examined, the ratio between the distal cell and the basal cell varied from 1.1:1 to 1.5:1. In *L. sorghoidea*, the basal cell was usually somewhat longer than the distal cell, the ratio varying from 1.2:1 to 1:1.2.

Angular prickle-hairs are present on the margins of all *Lasiacis* leaves. Prickle-hairs may also be present on the surface of the blade lamina, in which case they usually occur in rows interspersed among the short cells of the costal zone (Fig. 18). In *L. sloanei*, prickle-hairs were found in the intercostal zone.

Macrohairs vary greatly in size and shape. Their base is usually deeply sunken in the leaf surface and is surrounded by cushions of large cells (Fig. 9).

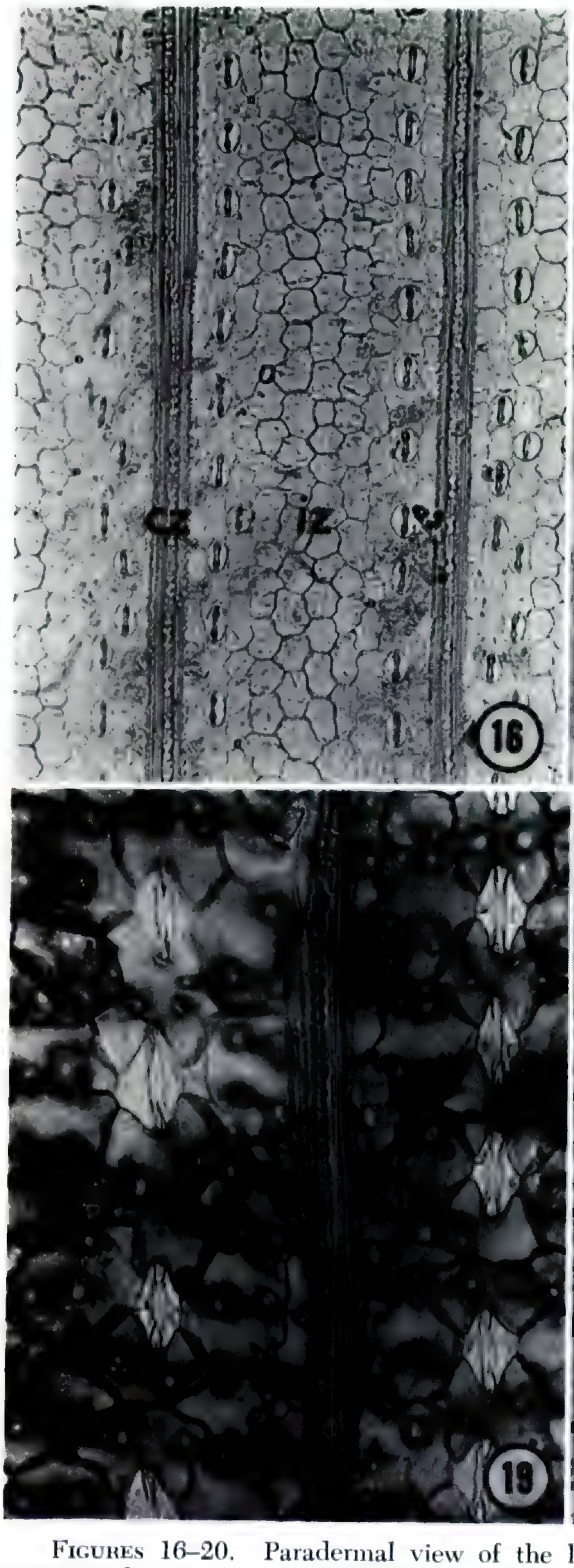
DISCUSSION

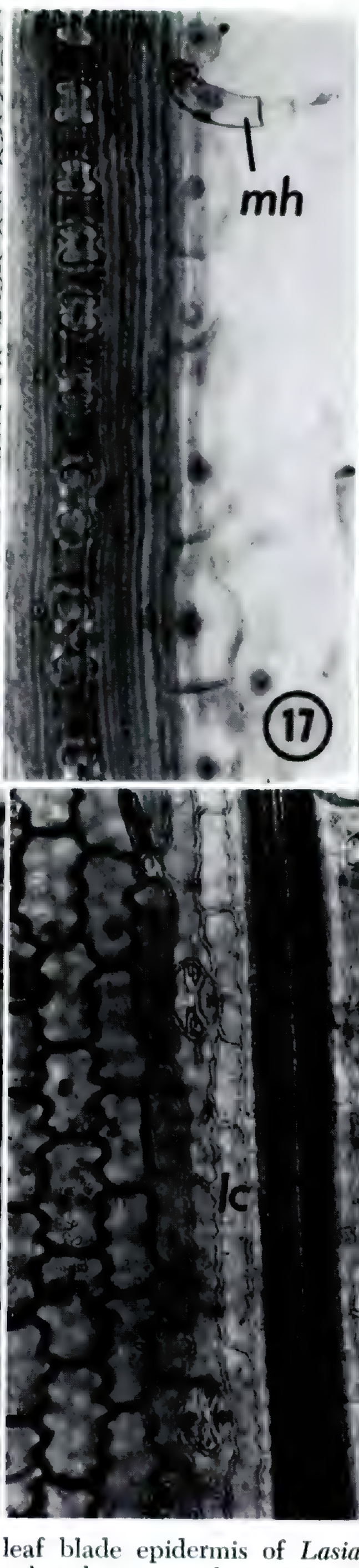
Anatomical characterization of the Panicoideae and the Bambusoideae has been made by Prat (1936), Brown (1958), Metcalfe (1960), and Gould (1968), among others. *Lasiacis* appears to be typically panicoid in the following characters: Angular SVBs, radiate chlorenchyma, short cells of costal zones in long rows, dumbbell- and nodular-shaped silica bodies, macrohairs with sunken bases, bicellular microhairs with thin-walled, tapering distal cells, and triangular- or dome-shaped subsidiary cells. In no anatomical characters is *Lasiacis* bambusoid. The contentions of Nuñez (1952) and Hsu (1965) of similarity to the bamboos in leaf anatomy must, therefore, he rejected. In their possession of an outer parenchyma bundle sheath whose cells have relatively large vacuoles, little cytoplasm, and few unspecialized chloroplasts, and in their possession of a starch-storing mesophyll differentiated into a palisade and spongy layer, all species examined have a non-Kranz anatomy that clearly indicates C_3 photosynthesis (Ellis, 1974; Smith & Brown, 1973). This agrees with the observations of Carolin & Jacobs (1973) who found *L. procerrima* to be non-Kranz on the basis of its parenchyma sheath, as did Smith & Brown (1973) on the basis of an analysis of carbon isotope ratios.

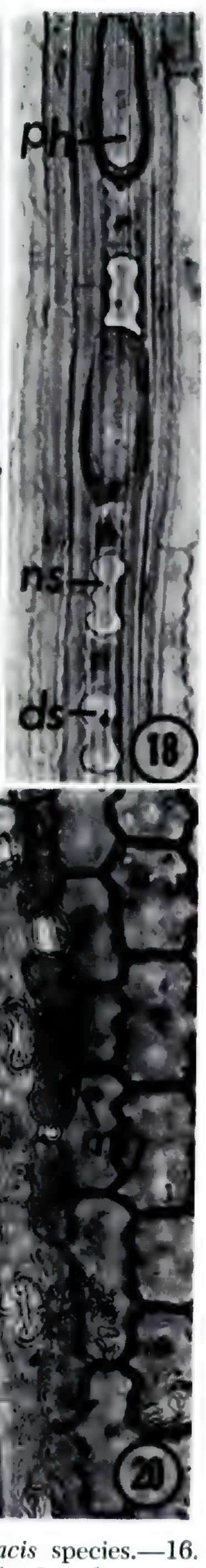
Breeding System

No information corncerning the breeding system of *Lasiacis* has been published. The following observations have been made in the greenhouse and in the field.

Anthesis in all species takes place in the morning, whether the plants are in the field or in the greenhouse. During anthesis, the lodicules force the lemma and palea of the fertile floret wide apart. This enables the coiled styles and filaments to straighten and to exsert the stigmas and anthers from the spikelet.







FIGURES 16–20. Paradermal view of the leaf blade epidermis of *Lasiacis* species.—16. Lower epidermis of *L. procerrima*; note the costal and intercostal zones.—17. Costal zone in the lower epidermis of *L. nigra*.—18. Costal zone in the upper epidermis of *L. scabrior*.—19. Lower epidermis of *L. rhizophora*.—20. Upper epidermis of *L. sloanei*. Abbreviations: cz = costal zone; ds = dumbbell-shaped silica body; iz = intercostal zone; lc = long cell; mh = microhair; ns = nodular-shaped silica body; ph = prickle-hair; sh = short cell.

TABLE 4. Determination of self-compatibility and percent of spontaneous fruit-set in isolated plants of *Lasiacis*.

Species	No. of collections tested for self-compatibility	No. of spikelets counted	% fruit-set
L. anomala	3	150	80
L. divaricata	7	380	90
L. linearis	1	25	60
L. procerrima	3	210	5
L. rhizophora	2	80	55
L. ruscifolia	5	500	95

The stigmas and anthers are always exserted simultaneously. Soon after exsertion, the spikelet closes again. When fully exserted, the anthers hang down on slender filaments and may be shaken in the wind. Pollen is then released into the air from a slit near the apex of the anther. Anther dehiscence is dependent upon environmental conditions, especially soil moisture and atmospheric humidity. Under dry conditions, dehiscence may take place very soon after exsertion of the anthers. Under hot, very humid conditions or in rain, dehiscence may be greatly or completely retarded. The feathery stigmas are receptive within an hour after exsertion.

All species tested in the greenhouse (Table 4) proved to be self-compatible. Self-compatibility, simultaneous exsertion of stigmas and anthers, simultaneous pollen release, and simultaneous stigmatic receptivity suggest that selfing is the dominant mode of pollination. Controlling pollination by isolating plants showed this to be the case. Fruit-set under these conditions usually varied from 55–95%. *Lasiacis procerrima* was notable in its 5% fruit-set. Even hand pollination between different plants of *L. procerrima* failed to improve fruit set appreciably. It is possible that stigmas may be receptive much later than in the other species, but this has not been investigated.

Self-pollination under natural conditions is undoubtedly the most important mode of pollination. A certain amount of cross-pollination probably also takes place. This is especially expected in crowded, dense populations where inflorescences of different plants would often intermingle. Under such conditions, wind-borne pollen would facilitate cross-pollination. Even then, pollination within an inflorescence is still most likely. Furthermore, in such populations most plants might be expected to have been derived from seed formed by self-pollination. Intrapopulational genetic diversity would, therefore, be low, and occasional outcrossing would not be highly effective in maintaining genetic variability. No information is available on the competition of foreign pollen with pollen from the same plant as the stigmas. If foreign pollen had a competitive advantage, this might increase the effectiveness of the small amount of cross-pollination that takes place.

One factor that may tend to increase the chance of cross-pollination is the

occurrence of staminate flowers in the sterile florets of some species. In the greenhouse, it is not uncommon to find only anthers from these staminate flowers exserted on a particular day. In a natural population, this could effectively increase the amount of pollen available for cross-pollination.

Deviation from the typical process of anthesis and pollination may take place. This results from the failure of the stigmas and anthers to be fully exserted at anthesis. When this happens, usually only the tips of the anthers and stigmas emerge from the spikelet. Less commonly, the anthers and stigmas remain entirely included within the lemma and palea after it closes again. The opening and closing of the lemma and palea can cause dehiscence of the anthers and may effectively distribute pollen on the stigmas. Such pseudocleistogamy has been observed in occasional spikelets of most greenhouse plants.

Grasses are generally recognized as anemophilous plants. However, some tropical forest grasses are pollinated, at least in part, by insects (Soderstrom & Calderón, 1971). Even some temperate-zone grasses such as *Zizania aquatica* are sometimes visited by bees collecting pollen (Thieret, 1971). I have not observed any insect visitation to any *Lasiacis* species in the field. If such visits do occur, effective pollination, especially cross-pollination, would probably seldom take place.

As with the majority of flowering plants (Baker, 1959), *Lasiacis* species have a system of mixed outbreeding and inbreeding, with inbreeding the dominant force. With such a predominantly autogamous breeding system, variation within local populations is theoretically expected to be minimal (Baker, 1959; Grant, 1971), and this is what is observed in the field. Occasional outcrossing would, however, presumably be adequate to maintain a fairly high level of genetic variability in the species as a whole.

CHROMOSOME NUMBERS

New chromosome number determinations for 101 collections of *Lasiacis* are listed in Table 5. Also included in Table 5 are previous reports of chromosome numbers for ten collections representing six species (Parodi, 1946; Nuñez, 1952; Tateoka, 1962; Gould & Soderstrom, 1967, 1970; Reeder, 1967, 1968). Of the 16 species recognized in this study, 3 (*L. grisebachii*, *L. rugelii*, and *L. scabrior*) remain cytologically unknown.

Reeder (1968) reported *L. sloanei* to have $n = 18$. However, the plant upon which it is based is the glabrous form of *L. nigra*. The voucher lacks the long, well-separated panicle branches of *L. sloanei*, and the spikelets are not short-pedicelled and appressed to the panicle branches. Furthermore, the spikelets are purple, a character unknown in *L. sloanei*, and the leaves lack the short, densely puberulent pseudopetiole of *L. sloanei*.

The counts reported by Parodi (1946) and Nuñez (1952) were probably based on *L. divaricata* var. *austroamericana*, since only this variety of *L. divaricata* occurs in Argentina. I have not seen any voucher specimens for these counts.

The chromosome number $n = 18$ has now been determined for 111 collections of *Lasiacis*. Pairing was complete and no irregularities were noted in my prepara-

TABLE 5. Chromosome numbers and voucher specimens for *Lasiacis* species.

L. anomala; $n = 18$[a]

VENEZUELA: Bolívar: 13 km ESE of Upata, *D et al. 4617*. Guárico: 10 km SSE of Calabozo, *D 2916*, *D 3690*; 5.5 km W of Guayabol, *D 3001*; 80 km S of Las Mercedes, *D 4272*. TRINIDAD: 2 mi NE of Piarco, *D 2591*, *D 2591B*, *D 2592*; Between Piarco and Piarco Int. Airport, *D 2522B*, *D 2523A*; Irois Bay, *D 2580A*.

L. divaricata var. *divaricata*; $n = 18$, $2n = 36$[a]

NICARAGUA: Zelaya: Río Coco at Bilwaskarma, *DP 2295A*. HONDURAS: Atlantida: 17 km SSE of La Ceiba, *DP 2196A*.[b] JAMAICA: St. Thomas Parish: 2.3 mi N of Eleven-Mile Intersection, *D & Conroy 3258*.[b] DOMINICAN REPUBLIC: Barahona: 12 km NNE of Polo, *D 2721*. UNITED STATES: Florida: Monroe Co., 10 mi NE of Flamingo, *Weatherwax*.

L. divaricata var. *austroamericana*; $n = 18$, $2n = 36$

ARGENTINA, no vouchers indicated (Parodi, 1946; Nuñez, 1952).[c] BRAZIL: São Paulo: Ca. 38 km SW of Jacupiranga, *D et al. 10948*.

L. harrisii; $n = 18$[a]

JAMAICA: Portland Parish: Muriel's Rock, *D & Proctor 3242*.

L. ligulata; $n = 18$

SURINAM: Zuid Rivier, *Irwin et al. 55790B*[d] (Gould & Soderstrom, 1967). COLOMBIA: Caquetá: *Soderstrom 1415*[e] (Gould & Soderstrom, 1970). BRAZIL: Minas Gerais: Ca. 8 km N of Teófilo Otoni, *D et al. 11500*; Ca. 27 km SE of Coroaci, *D et al. 11477*.

L. linearis; $n = 18$[a]

HONDURAS: Morazán: Cerro La Tigre, 11 km NE of Tegucigalpa, *DP 2121*; Cerro Uyuca, *DP 2100C*, *DP 2106*.

L. nigra; $n = 18$

MEXICO: San Luis Potosí: 41 mi W of San Luis Potosí, *Reeder & Reeder 4765*[f] (Reeder, 1968). Michoacán: Ca. 1.7 mi NW of Tuxpan, *DD 9819*. Chiapas: Ca. 8 mi NE of Solistohuacan, *DD 9458*. EL SALVADOR: Libertad: Volcán de San Salvador, *DP 2025*. HONDURAS: Morazán: Cerro La Tigre, 10 km NE of Tegucigalpa, *DP 2119*. El Paraíso: 7 km NW of San Lucas, *PD 12161*. COSTA RICA: Alajuela: 10 km N of San Ramón, *PD 11275*. Cartago: Moravia de Chirripó, *PD 11870*; 25 km SW of Tejar, *PD 11134*. San José: 2 km NNE of San Gabriel, *PD 11051*. PANAMA: Chiriquí: E slope of Volcán de Chiriquí, *D & D'Arcy 10155*. VENEZUELA: Aragua: Rancho Grande, *D 3033*; Alto de Choroní, *D 3100*. Distrito Federal: Rd. to Carayaca, *D & Morillo 3999*. Mérida: 66 km NE of Mérida, *D 3240*.

L. oaxacensis var. *oaxacensis*; $2n = 36$[a]

EL SALVADOR: Libertad: Volcán de San Salvador, *DP 2026A*.[b]

L. oaxacensis var. *maxonii*; $2n = 36$[a]

HONDURAS: Yoro: 15 km SSE of Río Viejo, *DP 2199A*.[b]

L. procerrima; $n = 18$, $2n = 36$[a]

MEXICO: Chiapas: 5 mi N of Ixtacomitan, *DD 9435*. EL SALVADOR: Chalatenango: 7 km SSE of La Palma, *DP 2072*. NICARAGUA: Zelaya: Intersection of Waspam-Puerto Cabeza Rd. and Río Lecus, *DP 2347*, *2347A*,[b] *PE 12701*. HONDURAS: Morazán: Between San Juancito and Valle de Angeles, *DP 2125*; Between El Zamorano and San Antonio de Oriente, *DP 2161*. El Paraíso: 32 km W of Danlí, *DP 2146*. COSTA RICA: Guanacaste: 8 km E of Liberia, *PD 10639*; 10 km NE of Las Juntas, *PD 10960*. Puntarenas: Near San Vito de Java, *PD 11163*. COLOMBIA: Caquetá: Florencia, *Soderstrom A*, *C*, *E*; 70 km SE of Guadalupe, *D et al. 5638*. Cundinamarca: 20 km NW of Villavicencio, *D & Llanos 5523*. VENEZUELA: Bolívar: La Gran Sabana, *D et al. 4783*.

L. rhizophora; $n = 18$, $2n = 36$

MEXICO: Chiapas: Sierra Madre, *Tateoka 1030*[b,d] (Tateoka, 1962). HONDURAS: El Paraíso: 8 km W of Yuscaran, *PE 12748*. Morazán: Cerro Uyuca, *P 12489*, *P 12489A*. COSTA RICA: San José: S of Curridabat, *PD 11694A*; 1 mi N of San Gabriel, *PD 11179*. PANAMA: Chiriquí: E slope of Volcán de Chiriquí, *D & D'Arcy 10158*.

TABLE 5. (Continued)

L. ruscifolia var. *ruscifolia*; $n = 18$, $2n = 36$

MEXICO: Chiapas: Mapestepec, *Tateoka 1001*[b, d] (Tateoka, 1962); Ca. 2 mi NW of the Tehuantepec-Tapachula intersection, *DD 9571*. Veracruz: Santiago Tuxtla, *Reeder 4333*[e] (Reeder, 1967). San Luis Potosí: Near Xolol, *PD 11808*, *PD 11808B*. EL SALVADOR: Santa Ana: 11 km E of Metapán, *PE 12583*. HONDURAS: Atlantida: 9 km E of Tela, *DP 2188*. Cortes: 1 km S of Puerto Cortes, *DP 2169*. COSTA RICA: Guanacaste: Hacienda Murciélago, *PD 11562A*. Puntarenas: 1.5 km S of the Puntarenas-Interamerican Highway jct., *PD 11278*. COLOMBIA: Caquetá: *Soderstrom 1415*[e] (Gould & Soderstrom, 1970). VENEZUELA: Guárico: 14 km N of Dos Caminos, *D 3012*;[b] 15 km SW of Tamaco, *D 4220*.

L. ruscifolia var. *velutina*; $n = 18$[a]

HONDURAS: Morazán: Between El Zamorano and San Antonio de Oriente, *DP 2162*.

L. sloanei; $n = 18$[a]

MEXICO: Oaxaca: 8 mi NE of Valle Nacional, *DD 9732*. HONDURAS: Yoro: 19 km SE of Río Viejo, *DP 2200*. COSTA RICA: Guanacaste: 30 km N of Cañas, *PE 12637*. Puntarenas: Road to Boruca, *PD 10994*.

L. sorghoidea var. *sorghoidea*; $n = 9$

COLOMBIA: Caquetá, *Soderstrom 1407*[d] (Gould & Soderstrom, 1970).

L. sorghoidea var. *sorghoidea*; $n = 18$, $2n = 36$[a]

COSTA RICA: Puntarenas: Finca Las Cruces, near San Vito de Java, *PD 10790C*.[b] PANAMA: *Morton B*. VENEZUELA: Amazonas: Isla Carestía, 5 km NNW of Sanariapo, *D 2875*; 12.5 km S of Puerto Ayacucho, *D 2785*; 20 km S of Puerto Ayacucho, *D 2839*. Apure: 42 km NW of Achaguas, *D et al. 3923*. Bolívar: La Gran Sabana, *D et al. 4782*; El Pao Viejo, *D et al. 4968*. Barinas: 43 km NW of Barinas, *D 3194*; 31 km NW of Barinas, *D 3184*. Distrito Federal: 19.8 km S of Carayaca, *D 2902*. Guárico: 10 km S of San Juan de los Morros, *D 3015*. Portuguesa: 20 km NE of Guanare, *D 3149*. COLOMBIA: Caquetá: 55 km SE of Guadalupe, *D et al. 5629*; 10 km SW of Belén, *D et al. 5690*; 8 km SW of San José del Fragua, *D et al. 5727*. Cundinamarca: 20 km NW of Villavicencio, *D & Llanos 5522*. Huila: 6 km SE of Altamira, *D et al. 5585A*; 10 km SE of Guadalupe, *D et al. 5605*. JAMAICA: St. Andrew Parish: Silver Hill, *D & Proctor 3247*; Above Gordon Town, *D & Proctor 3250*.

L. sorghoidea var. *patentiflora*; $n = 18$[a]

VENEZUELA: Mérida: 32 km NE of Mérida, *D 3232*. COLOMBIA: Caquetá; 15 km SW of Belén, *D et al. 5692*.

L. standleyi; $n = 18$[a]

COSTA RICA: San José: Between La Hondura and La Palma, *PD 11210*.

[a] First count recorded for this taxon.
[b] Root tip count.
[c] Originally reported as *L. divaricata* (see text).
[d] Voucher seen.
[e] Voucher not seen.
[f] Originally reported as *L. sloanei* (see text).

tions (Figs. 21–22) nor have previous authors reported any irregularities. For one collection of *L. sorghoidea* from the Florencia region of Caquetá, Colombia, the number $n = 9$ has been reported (Gould & Soderstrom, 1970). This diploid is morphologically similar to tetraploids of the same species.

From this limited sample, it seems clear that *Lasiacis* populations are basically tetraploid. It can also be reasonably surmised that most of the speciation has taken place at this level and that polyploidy, after its initial establishment in the ancestral species of the genus, has played little or no further part in the evolution

FIGURES 21–22. Meiotic chromosomes of *Lasiacis* species.—21. *L. sorghoidea* var. *sorghoidea*, *Morton B*, $n = 18$, diakinesis.—22. *L. linearis*, *Davidse & Pohl 2121*, $n = 18$, metaphase I.

of the group. The genus as a whole seems to have become secondarily diploidized at the 4*x* level.

The single diploid count reported by Gould & Soderstrom (1970) for *L. sorghoidea* from Caquetá, Colombia, is surprising since all other counts now known are at the tetraploid level. I have examined four other populations of *L. sorghoidea* from the region in Florencia in Caquetá, Colombia, and found all to be tetraploid. This suggests that an error may have been involved in the report of the diploid count. Another possibility is that the presumed diploid represents a secondary derivative through haploidization. Raven & Thompson (1964) and de Wet (1971) have pointed out that there is no theoretical reason why haploidy, and in particular polyhaploidy, could not have played a role in the evolution of some plant groups. However, without more evidence, it is best not to place too much importance on this single diploid count.

The Paniceae typically have a base number of $x = 9$ or 10 and small- or medium-sized chromosomes (Stebbins, 1956; Gould, 1968). In this respect *Lasiacis* is typically panicoid. All species investigated have a base number of $x = 9$ with medium-sized chromosomes; Nuñez (1952) after studying mitotic chromosomes of *L. divaricata* stated that its chromosomes were larger than any panicoid studied by him except *Pennisetum*. My impression on the basis of studying meiotic chromosomes of a large number of American tropical grasses (Pohl & Davidse, 1971; Davidse & Pohl, 1972a, 1972b, 1974, 1978) is similar. *Lasiacis* chromosomes are among the largest of the American Paniceae, but are distinctly smaller than those of typical Pooideae.

TAXONOMY

Lasiacis (Griseb.) Hitchc., Contr. U.S. Natl. Herb. 15: 16. 1910.

Panicum sect. *Lasiacis* Griseb., Fl. Brit. W. Ind. 551. 1864. TYPE: *Panicum divaricatum* L. = *Lasiacis divaricata* (L.) Hitchc.

Plants perennial, rarely annual in *L. procerrima*; culms freely branched, caespitose, highly lignified and erect, arching or climbing, or procumbent and nearly herbaceous, creeping, and rooting the nodes; internodes solid or hollow; culm pulvini well developed; sheaths rounded, the margins free and overlapping; ligules membranous, ciliate or glabrous; collar sometimes somewhat enlarged to form a small pseudopetiole; blades linear to ovate, slightly to prominently asymmetrical at the base; inflorescence an open or contracted panicle; spikelets subglobose to globose, obovate or elliptic, placed obliquely on the pedicel; disarticulation below the glumes; glumes and sterile lemmas broad, abruptly apiculate, membranous, shiny black at maturity, lanate at the apex; first glume ⅓ to ⅔ the length of the spikelet, 5- to 13-nerved, saccate at the base, the margins overlapping; second glume and sterile lemma subequal, about as long as the fertile floret, 7- to 15-nerved, the sterile lemma enclosing a palea ¼ to equal the length of the fertile floret; sterile floret with or without a staminate flower; a second sterile lemma present in *L. anomala*; cells of the inner epidermis of the glumes and sterile lemmas filled with oil globules at maturity; fertile lemma indurate, obtuse, the margins inrolled enclosing the edges of the indurate palea, usually dark brown at maturity, broadly elliptic to obovate; palea gibbous above, concave below, its margins lobed, overlapping or meeting on the dorsal side of the caryopsis; both fertile lemma and palea with woolly pubescence in slight excavations at their apices; rachilla sometimes prolonged beyond the base of the fertile floret; stamens 3; styles 2, the bases separate; lodicules 2, fleshy, truncate, vasculated, 1 limb within the fertile palea, the other situated between the fertile lemma and palea; caryopsis plano-convex, ovate, obovate, or nearly orbicular, the apex rounded, sometimes broadly grooved on the hilum side; hilum oblong or nearly round; embryo approximately ½ the length of the caryopsis.

Lasiacis forms a natural, distinct group whose generic rank has not been questioned since Hitchcock & Chase (1910) raised the group to generic level. Although the basic spikelet structure of *Lasiacis* is similar to that of *Panicum*, *Lasiacis* does possess and is characterized by a number of distinctive modifications of that basic type. These characters are the nearly globose spikelets borne obliquely on the pedicels, woolly pubescence at the apex of the spikelet bracts, black coloration at maturity, oil production in the inner epidermis of the glumes and sterile lemmas at maturity, broadly ovate to obovate fertile florets and caryopses, and the fertile paleas concave below and gibbous above.

In previous sections, I have shown that *Lasiacis* is typically panicoid in features of vegetative and spikelet morphology, leaf anatomy, and chromosome number and size. Reeder (1957) in his classic study of grass embryos showed that *Lasiacis* is typically panicoid in embryo morphology also. The embryo is characterized by the possession of a distinct internode between the coleoptile

and scutellum, a cleft between the scutellum and coleorhiza, a primary leaf with numerous vascular bundles and overlapping margins, and the absence of an epiblast (Reeder, 1957).

Hsu (1965) in his studies of genera of Paniceae determined *Lasiacis* to have the following characteristics: bony-indurate, smooth lemmas; lemmatal epidermis with longitudinally rippled ridges, microhairs, and two to four aggregate granular silica cells; plicate, somewhat corky lodicules with numerous vascular bundles; distinct style bases; punctiform hilum. Hsu believed all these to be unspecialized characters and on this basis considered *Lasiacis* to be among the most primitive genera in the tribe. He further determined *Acroceras* and *Commelinidium* to be closely related to *Lasiacis* and speculated that *Lasiacis* probably resembles the ancestor of the tribe more closely than any other extant genus.

Butzin (1970a, 1970b) has proposed a new subtribe, Microcalaminae, of the Paniceae, based largely on the presence of cross-veins in the leaves, but also on inflorescence type, spikelet compression, and orientation of the lemmas. Included are *Lasiacis*, *Acroceras*, *Commelinidum*, and 16 other genera. This subtribe is considered to be phylogenetically basal in the tribe, with *Lasiacis* being one of the most primitive genera (Butzin, 1970a, 1970b).

If, as Butzin and Hsu have done, one assumes that the Paniceae arose from a generalized bambusoid stock which had woody culms, cross-nerved leaves, large diffuse panicles, spikelets round in cross-section, awnless lemmas, and indurate fertile florets, then *Lasiacis* should indeed be considered primitive. It may further be noted that such an ancestral stock probably had more than two florets per spikelet. The tendency to produce extra bracts in some *Lasiacis* species (an extra sterile lemma in *L. anomala*, and sterile projections at the base of the fertile floret, representing an extra fertile floret, in *L. ruscifolia* and *L. grisebachii*) further strengthens the speculative relationship with a primitive bambusoid stock.

In most Spanish-speaking countries, *Lasiacis* species are generally known by the name *carrizo* or the diminutive *carricillo*. The name is not used for *Lasiacis* alone but is employed in a collective sense for large woody, scandent grasses such as some of the bamboos and *Olyra*. In Portugese, the name *taquarí* seems to be employed in the same sense. Standley & Record (1936) reported that the Mayan word for these kinds of grasses is *zit*. Other, more local names, are listed after the species for which it has been reported.

Key to the Species

1. Spikelets with 2 glumes and 2 sterile lemmas subtending the fertile floret .... 1. *L. anomala*
1′. Spikelets with 2 glumes and 1 sterile lemma subtending the fertile floret.
  2. Culms solid, pithy; plants normally creeping and rooting at the lower nodes.
    3. Ligules inconspicuous, 0.4–1.1 mm long, ciliate; leaf blades lanceolate, 8–13 (–17) cm long, 1.6–3.7 cm wide ..... 10. *L. rhizophora*
    3′. Ligules conspicuous, 1.4–6.0 mm long; leaf blades linear-lanceolate, 13–29 cm long, 0.8–2.4 cm wide.
      4. Sheaths glabrous; spikelets borne in pairs or singly in small clusters toward the end of the panicle branches; lower floret usually staminate, its palea subequal in length to the fertile floret.
        5. Ligules (2.0–)2.6–5.0(–6.0) mm long ..... 8a. *L. oaxacensis* var. *oaxacensis*
        5′. Ligules 0.5–1.5 mm long ..... 8b. *L. oaxacensis* var. *maxonii*

4′. Sheaths puberulent to pubescent; spikelets borne singly on long pedicels toward ends of the panicle branches; lower floret lacking a flower, its palea ⅔ or usually less the length of the fertile floret ..... 6. *L. linearis*

2′. Culms hollow or partially hollow with some pith remnants; plants creeping and rooting at the lower nodes, or erect, arching, and/or climbing.

6. Plants creeping and rooting at the lower nodes.

7. Ligules inconspicuous, 0.3–0.7 mm long; sterile palea equal or subequal in length to the fertile floret.

8. Blades 0.6–1.1(–1.4) cm wide ..... 3a. *L. grisebachii* var. *grisebachii*

8′. Blades 1.5–2.0 cm wide ..... 3b. *L. grisebachii* var. *lindelieana*

7′. Ligules conspicuous, (4.5–)5–7(–9.0) mm long; sterile palea less than ½ the length of the fertile floret ..... 16. *L. standleyi*

6′. Plants erect.

9. Leaf blades conspicuously cordate-clasping, (14–)18–32(–42) cm long; lower nodes decumbent, forming conspicuous prop roots; inflorescences (20–)32–120 cm long ..... 9. *L. procerrima*

9′. Blades not conspicuously cordate, smaller, 2.5–14(–18) cm long; plants without conspicuous prop roots; inflorescences smaller, 2–30(–34) cm long.

10. Ligule of the upper leaves evident, (1.6–)2.0–6.0(–7.0) mm long.

11. Panicle spherical, small, usually less than 9 cm long, the base included in the upper sheath, only rarely completely exserted; upper surface of the blade scabrous; ligule mostly 4–6 mm long ..... 13. *L. scabrior*

11′. Panicle ovoid, larger, (2–)9–25(–30) cm long, the base usually completely exserted; upper surface of blades glabrous, or variously pubescent; ligules mostly less than 3.5 mm long.

12. Panicle branches reflexed or widely spreading; sheaths puberulent or glabrous; blades mostly 7–14 cm long, 1.0–2.2 cm wide ..... 5. *L. ligulata*

12′. Panicle branches ascending to spreading; sheaths papillose-hispid or pubescent; blades mostly 9–19 cm long, 1.2–3.4 cm wide ..... 15a. *L. sorghoidea* var. *sorghoidea*

10′. Ligule of upper leaves not readily visible, but if evident, mostly less than 1.5 mm long.

13. Blades glabrous on both surfaces, sometimes with a few small scattered hairs at the base of the upper and/or upper and lower surfaces ..... 2b. *L. divaricata* var. *austroamericana*

14. Blades linear to narrowly lanceolate, mostly less than 2 cm wide.

15. Panicle bearing few spikelets, the lower panicle branches reflexed or widely spreading; pedicels sharply divergent at maturity; culms zigzag ..... 2a. *L. divaricata* var. *divaricata*

15′. Panicle various, but the lower panicle branches mostly not reflexed; culms straight or zigzag.

16. Spikelets 4.0–5.0 mm long.

17. Base of the panicle included in the sheath; pedicels and panicle branches short ..... 2c. *L. divaricata* var. *leptostachya*

17′. Base of the panicle usually exserted; pedicels slender, widely spreading, somewhat flexuous ..... 7. *L. nigra*

16′. Spikelets 3.4–4.1(–4.3) mm long.

18. Blades 0.3–0.7 cm wide; Jamaican endemic ..... 4. *L. harrisii*

18′. Blades 0.6–1.8(–3.0) cm wide; South America ..... 2b. *L. divaricata* var. *austroamericana*

14′. Blades ovate to broadly lanceolate, mostly more than 2 cm wide.

19. Main inflorescence branches sparsely branched, bearing few, large spikelets (3.6–)4.0–5.0(–5.3) cm long.

20. Pedicels short, appressed; blades (1.3–)1.7–4.0(–4.5) cm wide, with a short, densely puberulent pseudopetiole 1–3 mm long ..... 14. *L. sloanei*
20′. Pedicels longer, widely spreading; blades (0.3–)0.6–1.8(–2.6) cm wide, without the short, characteristic pseudopetiole ..... 7. *L. nigra*

19′. Main inflorescence branches highly branched, bearing numerous, smaller spikelets (2.6–)2.8–4.1 cm long.
21. Spikelets globose, the base of the fertile lemma usually with a distinct shelf from which a sterile projection often arises; blades of the main culms ovate to ovate-lanceolate; spikelets densely arranged ..... 12a. *L. ruscifolia* var. *ruscifolia*
21′. Spikelets not globose, more elongated, the base of the fertile lemma without a shelf; blades of the main culms lanceolate, spikelets less densely arranged ..... *L. sorghoidea* var. *patentiflora*

13′. Blades with some pubescence on at least one surface.
22. Blades small, relatively short and broad, ovate, 2–7(–9.5) cm long, (0.5–)0.8–2.8 cm wide, densely arranged on the branches.
23. Upper blade surface hispid, velutinous, or pilose; panicle branches densely pilose ..... 12b. *L. ruscifolia* var. *velutina*
23′. Upper blade surface glabrous to puberulent; panicle branches usually scabrid, puberulent, or with a short pubescence, only rarely pilose.
24. Culms papillose-pubescent or papillose-puberulent throughout; panicle branches reflexed; spikelets 4.0–4.8 mm long, obovate ..... 11a. *L. rugelii* var. *rugelii*
24′. Culms glabrous or with a line of puberulence, not papillose-puberulent throughout; panicle branches ascending to spreading; spikelets 3.6–4.2 mm long, globose ..... 11b. *L. rugelii* var. *pohlii*

22′. Blades larger, linear-lanceolate to ovate, (5–)6–25(–35) cm long, (0.3–)0.6–4.4(–5.6) cm wide, relatively widely separated on the branches.
25. Spikelets (3.6–)4.0–5.0 mm long; panicle rather open with few spikelets, the pedicels widely spreading ..... 7. *L. nigra*
25′. Spikelets (2.6–)2.8–4.1 mm long; panicle much denser, the pedicels not as widely spreading.
26. Spikelets obovate; leaves typically with the following combinations of pubescence, the upper blade surface puberulent, the lower surface velutinous, the collar densely hispid, and the sheath papillose-hispid, sometimes the foliage only puberulent; blades usually linear-lanceolate to lanceolate, typically proportionally longer and narrower; inflorescences open, generally larger, (5–)9–25(–35) cm long; spikelets (3.0–)3.4–4.1(–4.3) mm long ..... 15a. *L. sorghoidea* var. *sorghoidea*
26′. Spikelets usually globose; leaves only rarely with the above combination of pubescence, glabrous to hispid or villous; blades usually lanceolate-ovate to ovate, proportionally shorter and broader; inflorescences dense, generally smaller, (2–)4–16(–22) cm long; spikelets (2.6–)2.8–3.8(–4.0) mm long ..... 12a. *L. ruscifolia* var. *ruscifolia*

1. **Lasiacis anomala** Hitchc., J. Wash. Acad. Sci. 9: 37. 1919. TYPE: Trinidad, Fort George Road, Port of Spain, edge of jungle, high climbing, with strong

central cane, the branches not fascicled, main culm thick as pencil, 27 Nov. 1912, *Hitchcock 9977* (=Amer. Grass Natl. Herb. No. 595) (US, holotype; F, GH, MO, NY, P, US, isotypes).

Panicum latifolium var. *tomentellum* Doell in Mart., Fl. Bras. 2(2): 207. 1877. TYPE: Brazil, Ceará, *Gardner 1894* (K, lectotype; NY, P, US, isolectotypes).

Perennial; culms caespitose, 0.4–5.0 m long, lignified, erect and arching, commonly rather weak and supported in erect position by surrounding vegetation, small culms of young plants occasionally procumbent and then rooting at the nodes; internodes of main culms 3–9 mm thick, hollow, glabrous, those of the ultimate branches often with a dense to sparse line of puberulence; nodes glabrous; primary branches usually 1 per node, secondary and tertiary branches 1 per node to fascicled; sheaths usually puberulent, sometimes villous or hispid with hairs to 1.5 mm long, often becoming glabrate on the upper sheaths, rarely all sheaths glabrous, the upper margin and throat ciliate, the auricular hairs inconspicuous to 2.5 mm long; collar typically densely puberulent to hispid with hairs up to 1.2 mm long; ligule membranous, 0.3–0.8(–1.8) mm long; blades (2.5–)5–12(–15) cm long, 0.8–3.0(–4.0) cm wide, ovate to narrowly elliptic-lanceolate, the upper surface puberulent or pubescent, rarely glabrous, the lower surface usually densely, softly puberulent, occasionally hispid or glabrous, the apex abruptly acute to gradually acuminate, the base asymmetrical, ciliate, somewhat clasping, the margin scabrid; lower leaves of secondary and tertiary branches usually with more pronounced pubescence, the upper leaves of the main branch often becoming glabrate; panicles 2–15 cm long, the longest branch 1–4 cm long, with the spikelets rather evenly and compactly arranged on the branches, the branches ascending to widely spreading and reflexed, the lower ones well separated, minutely puberulent and scabrous, the pulvini puberulent to glabrous; spikelets (2.8–)3.1–3.5(–3.8) mm long, globose; first glume (1.0–)1.2–1.8 mm long, 7-nerved; second glume (2.0–)2.3–2.7 mm long, 9-nerved; first sterile lemma 9-nerved, without a sterile palea or a flower, subequal in length to the fertile floret; second sterile lemma 9-nerved, with a sterile palea ½ to ¾ the length of the fertile floret, usually without, sometimes with a staminate flower; fertile floret 2.6–2.9 mm long, 1.6–1.7 mm wide, blackish brown, the anthers 1.6–1.7 mm long, white, the stigma white; caryopsis 2.0–2.1 mm long, 1.5–1.6 mm wide, light brown; chromosome number $n = 18$.

Ecology: *Lasiacis anomala* typically inhabits savana areas or the drier tropical forests at elevations from sea level to 800 m. It occurs commonly along forest edges, in gallery forests, in brush of secondary forests, and in clumps of trees in savannas. Collections with spikelets have been made from late April to December.

Distribution: This species is found in north-central South America including eastern Colombia, Venezuela, Guyana, Surinam, and northern Brazil. It also occurs on the islands of St. Vincent, Barbados, Trinidad, and Margarita.

Lasiacis anomala is unique in having an extra bract (sterile lemma) in the spikelet and identification, therefore, causes no problem. Hitchcock (1919) discussed this species in detail. He considered it to be closely related to *L.*

ruscifolia, differing essentially only in the presence of the extra sterile lemma. This character plus the distinctive geographical range, which excludes *L. ruscifolia*, were cited by him as reasons for accepting this taxon at the specific level. The present study confirms this conclusion. Field studies of many populations in Trinidad and Venezuela showed that these plants occur in pure populations. Spikelets in all plants in each population examined had an extra sterile lemma.

As Hitchcock (1919) noted, the presence of a second sterile lemma is contrary to the typical spikelet structure in the tribe Paniceae. Although this is a very striking morphological feature, one might hypothesize that it could be the result of a very small genetic difference, possibly a one gene difference. However, hybridization with *L. ruscifolia* (unpubl.) indicated that the two taxa are probably reproductively isolated, and its seems likely that more than one gene is responsible for the spikelet differences between the two taxa. Although the sterility barrier was not complete, there was a significant reduction in the fertility of the hybrids. This, plus the morphological difference and distinct geographical distribution of these taxa, is evidence that they should be maintained at the specific level.

Plants of *L. anomala* are in most respects similar to *L. ruscifolia*, as noted by Hitchcock. However, the inflorescences are smaller and more compact, the leaves are consistently smaller and less variable in pubescence, and the plants are generally less robust but more straggling and scandent than in *L. ruscifolia*.

BARBADOS. Hopewell, *Johnson 1246* (NY).

BRAZIL. AMAZONAS: Rio Branco, *Kuhlmann 3358* (US). BAHIA: Serra do Curral Feio, *Harley 16991* (MO). *16913* (MO). CEARÁ: Baturité, *Eugenic 284* (RB, US). Without definite locality, *Gardner 1884* (NY, US), *1894* (P), *1889* (US). Baturité to Guaramirango, *Swallen 4419* (RB, US). Campo Grande, *Swallen 4516* (US), *4587* (RB, US). MARANHÃO: Caxias to Barra do Gorda, *Swallen 3554* (US).

COLOMBIA. VICHADA: La Venturosa, Río Meta, *Cuatrecasas 4191* (F, US).

GUYANA. Takuta River, *Smith 3131* (F, GH, MO, NY, US).

SURINAM. Ebbatop, *Amshoff 1563* (NY). Wilhelmina Gebergte, *Irwin et al. 54540* (MO, NY, UC, US), *55331* (MO, NY, UC, US), *55696* (MO, NY, UC, US); *Maguire et al. 54204* (MO, NY, UC, US); *Schulz 10461* (IJ). Near Wonotobo, *Stahel & Gonggrijp 2854* (US).

TRINIDAD. Vic. of Brighton, *Britton 2905* (NY, US). Moruga, *Broadway 2504* (F, US). Mayaro, *Broadway 2627* (F, ISC, M, US). Chaguaramas, *Broadway 6739* (MO, US). Monos, *Broadway 7447* (US). Point Gourde, *Broadway 8081* (A, US), *8083* (MO, US). Chaguaramas, *Broadway s.n.* (US). Look Out Hill, *Broadway s.n.* (F, GH, MO, NY, US). Vic. of Piarco, *Davidse 2522* (ISC, MO), *2523* (ISC, MO). Irois Bay, *Davidse 2580* (ISC, MO). Vic. of Piarco, *Davidse 2591* (ISC, MO), 2592 (ISC, MO). Port of Spain, *Hitchcock A.G.N.H. 595* (F, GH, MO, NY, US), *10001* (F, US). St. Joseph, *Hitchcock 10021* (US). Chacachacare, *Hitchcock 10063* (US). San Fernando, *Hitchcock 10117* (US). Vic. of Cedros, *Hitchcock 10136* (GH, US). Erin Savanna, *Soderstrom 1126* (NY, UC, US). St. George, Morne Catherine Rd., *Webster & Miller 9943* (US).

VENEZUELA. AMAZONAS: Bords de l'Orénoque, *Chaffanjon 190* (P). 12.5 km N of Puerto Ayacucho, *Davidse 2784* (ISC), *2786* (ISC, MO). 5 km N of Sanariapo, *Maguire et al. 36170* (NY, US, VEN). Maypures, *Muer 3636* (P). 10–30 km ESE of Puerto Ayacucho, *Steyermark et al. 113905* (MO). ANZOÁTEGUI: Pariaguán, *Pittier 14535* (US, VEN), *14538* (F, US, VEN). El Guácimo, *Pittier 15053* (US). ARAGUA: Cata, *Cardenas 499* (MO, MY). Rancho Grande, *Montaldo & Ramia 3310* (MY). Maracay, *Montaldo 3532* (NY). Near Ocumare, *Pittier 14162* (NY, US). BOLÍVAR: 21 km E of Río Caura, *Davidse 4469* (MO). 13 km ESE of Upata, *Davidse et al. 4617* (MO). 18 km N of Upata, *Gentry & Berry 14923* (MO). 1 km NW of Upata, *Steyermark 57686* (F, NY, US). 2 km SE of Los Patos, *Steyer-*

mark 86992 (VEN). E of Miamo, *Steyermark 88215* (NY, US). Hato El Pillar, *Trujillo 2278* (MY). Cerro Bolívar, *Wurdack 34398* (NY, US, VEN). CARABOBO: Cortado Yuma, *Box 3913* (MO, MY, VEN). Vic. of Valencia, *Pittier 9016* (GH, NY, US, VEN), *9062* (GH, NY, US, VEN). Lago de Valencia, *Trujillo 3815* (MY). FALCÓN: Cerro Santa Ana, Paraguana, *Curran & Haman 699* (VEN); *Lasser & Aristeguieta 3394* (VEN). GUÁRICO: Vic. of Calabazo, Estación Biológia, *Aristeguieta 4335* (VEN), *5623* (NY, VEN); *Castellanos 12* (VEN); *Davidse 2916* (ISC, MO). 16 km S of Calabozo, *Davidse 2970* (ISC, MO). 26 km S of Calabozo, *Davidse 2983* (ISC, MO). 5.5 km W of Guayabol, *Davidse 3001* (ISC, MO). 46 km NW of Calabozo, *Davidse 3007* (ISC, MO). 10 km SSE of Calabozo, *Davidse 3690* (MO). 54 km N of San Fernando de Apure, *Davidse et al. 3968* (MO). 80 km S of Las Mercedes, *Davidse 4272* (MO). Vic. of Calabozo, *Trujillo 8638* (MO, NY). LARA: Sabanas de Cujicito, *Saer 533* (F, VEN). MONAGAS: Santa Bárbara Camp, *Maguire et al. 27275* (NY, US, VEN). NUEVA ESPARTA: Isla Margarita, *Johnston 196* (GH); *Miller & Johnston 184* (F, GH, MO, NY, US). YARACUY: 5 km S de Bella Vista, *Agostini et al. 1808* (MO). Between Campo Elías and Alerachiche, *Aristeguieta & Foldats 1330* (VEN).

2a. **Lasiacis divaricata** (L.) Hitchc. var. **divaricata**, Contr. U.S. Natl. Herb. 15: 16. 1910.

Panicum divaricatum L., Syst. Nat., ed. 10. 2: 871. 1759. TYPE: Jamaica, *Browne s.n.* (LINN, holotype, microfiche of the Linnaean Herbarium, sheet 80.65, inscribed Br.).

P. bambusoides Desv. in Hamilt., Prodr. Pl. Ind. Occ. 10. 1825. TYPE: Puerto Rico, "habitat in Am. Equinoxi" (P, holotype, photograph US).

P. chauvinii Steud., Syn. Pl. Glum. 1: 68. 1854. TYPE: Guadeloupe, *Duchassaing s.n.* (P, holotype).

P. divaricatum var. *stenostachyum* Griseb., Fl. Brit. W. Ind. 551. 1864. TYPE: Jamaica, *March 20* (GOET, holotype, fragments US).

P. divaricatum var. *glabrum* Kuntze, Rev. Gen. Pl. 2: 784. 1891. TYPE: not indicated, not seen.

Perennial; culms erect, caespitose, (0.5–)1–5(–7) m long, lignified but rather weak, usually strongly arching and supported in brush, often bending to the ground when unsupported, the upper portion of the main culm and large primary and secondary branches usually zigzag; branches solitary or fascicled at the nodes; internodes hollow, 5–9 mm thick, glabrous or with a line of puberulence on one side, rarely puberulent throughout or at the apex only; nodes glabrous; sheaths usually glabrous, less frequently puberulent, especially on the internerves, the overlapping margin and throat ciliate with hairs to 3.0 mm long, the auricular hairs 0.3–2.0(–3.0) mm long; collar usually sparsely puberulent, rarely densely pubescent with hairs to 0.7 mm long or completely glabrous; ligule membranous, inconspicuous, and usually not directly visible, 0.2–0.6(–1.2) mm long, usually ciliolate with hairs 0.1–0.3(–0.5) mm long, occasionally glabrous; blades (3–)5–12(–16) cm long, (0.3–)0.6–1.4(–2.0) cm wide, linear-lanceolate or lanceolate, the upper surface glabrous except for some scabridity or puberulence along the lower part of the midrib, the lower surface glabrous, rarely minutely puberulent, especially at the base, the base asymmetrical, the margin scabrid, the apex acuminate; lower blades on the culms often deciduous, leaving the sheaths; panicles 2–12(–20) cm long, the longest branch 2–8(–12) cm long, bearing few, widely spaced spikelets, the branches, especially the lower, reflexed, the upper branches widely spreading, scabrid, or the lower portions puberulent, the pedicels widely divergent from the panicle branches, the lower pulvini usually puberulent, occasionally glabrous; spikelets (3.5–)3.7–4.3(–4.5) mm long, obovate; first glume (1.2–)1.4–2.0(–2.5) mm long, 7–11(–13)-nerved; second glume

9–11-nerved; sterile floret without a flower, the lemma 9–13-nerved, the palea subequal to ½ the length of the fertile floret; fertile floret 3.4–4.0 mm long, 1.9–2.4 mm wide, whitish to brown at maturity, the anthers ca. 2.0 mm long, white, the stigmas purple; caryopsis 2.2–2.4 mm long, 1.7–1.9 mm wide, whitish; chromosome number $n = 18$.

Ecology: *Lasiacis divaricata* var. *divaricata* occupies a wide range of habitats. In Florida it is usually found in hammocks, but it has also been occasionally collected in pinelands. In the West Indies the plants are found from the xerophytic coastal thickets and *Acacia* shrub communities to the more mesophytic pine forests of broadleaf forests. In Central America and Mexico it is most common along brushy borders of lowland broad leaf forests, although it also occurs in the pine forest. Plants have been collected primarily below 1,000 m, only rarely above this in Mexico. Spikelet-bearing plants have been collected throughout the year, but the majority have been collected from June to early March.

Distribution: *Lasiacis divaricata* var. *divaricata* is essentially a Caribbean species. It extends from the southern tip of Florida throughout most of the West Indies, becoming rare in Trinidad and Venezuela. It is also known from Mexico to Panama.

I have followed Chase & Niles (1962) in assigning *P. divaricatum* var. *glabrum* to synonymy under *L. divaricata* var. *divaricata*. I have not seen the specimens upon which the names were based, but since these were from the Caribbean area and were described as having glabrous leaves, this seems a reasonable disposition of the name.

Lasiacis divaricata var. *divaricata* is recognized by its usually glabrous (only rarely minutely puberulent), narrowly lanceolate, rather firm, glossy blades, short ligules that are usually not visible without opening the sheath, and panicles with reflexed branches bearing a few obovate spikelets.

Hitchcock (1920, 1936) and Swallen (1943, 1955a) have stressed the glabrous nature of *L. divaricata*, and for this reason, all small-leaved, glabrous plants from South America have usually been considered to belong to this variety. Little attention had been paid to inflorescence, spikelet, and ligule characters, in all of which these South American plants traditionally assigned to *L. divaricata* differ from var. *divaricata* as recognized by me. For this reason, those South American plants are recognized as a new variety (var. *austroamericana*), thus limiting var. *divaricata* to the West Indies and much of the immediate adjoining Caribbean continental area.

The majority of specimens from Central America, Mexico, Cuba, and occasional specimens from throughout the remaining areas of its range have distinctly puberulent sheaths, rather than the glabrous sheaths ascribed to this taxon by Hitchcock (1920, 1936). Some specimens from Chiapas (*Beetle M-3902*) and Belize (*Croat 23649, 23707*; *Dwyer 11155*) have papillose-puberulent internodes and in this respect resemble *L. divaricata* var. *leptostachya*.

Through many of the Lesser Antilles extending from Saba to Grenada, there occur plants with ligules primarily 0.6–1.0 mm long. These appear somewhat different from most plants of var. *divaricata* because the ligules can usually be

easily seen without moving the sheath back. The distinction seems hardly great enough to warrant varietal status. If this was desired, however, it should be noted that the type of *Panicum chauvinii* falls within this morphological group.

Common names: Hitchcock (1936) reports that this species is known as pito de bejuco in Cuba. Cuba: Santa Clara, tibisi, *Luna 206*. Bahamas: Conception Island, wild cane, *Britton & Millspaugh 60633*.

BAHAMA ISLANDS. ACKLINS ISLAND: *Brace 4305* (F, NY, US). ANDROS ISLAND: Deep Creek, *Brace 5108* (F, NY). Conch Creek, *Brace 6786* (F, NY). Deep Creek, *Northrop & Northrop 723* (F); *Small & Carter 8586* (F, NY, P, US). ANGUILLA ISLAND: Salt Key Bank, *Wilson 8051* (F, NY). CAT ISLAND: Wilson Bay, *Byrne 133* (A, WIS), *227* (WIS), *s.n.* (A). CONCEPTION ISLAND: *Britton & Millspaugh 6033* (F, NY). CROOKED ISLAND: Marine Vied Road, *Brace 4617* (F, NY). *Hitchcock s.n.* (MO). ELEUTHERA: Glass Window to Gregory Town, *Britton & Millspaugh 5405* (F, NY). Harbour Isle, *Britton 6403* (F, NY). *Rothrock 584* (F). GREAT ABACO ISLAND: Green Turtle Cay, *Brace 1509* (F, NY). Cherokee, *Brace 1908* (F). Green Turtle Cay, *Correll & Correll 47652* (MO). Near Treasure Cay, *Gillis 6134* (A). Lubbers Quarters, *Gillis 7338* (A). Wilson City, *Proctor 30706* (IJ). GREAT BAHAMA ISLAND: Barnett's Peak, *Britton & Millspaugh 2630* (F, NY). GREAT INAGUA: NW Point, *Dunbar 233* (A). LITTLE INAGUA: Whiteland, *Nash & Taylor 1240* (NY). LITTLE SAN SALVADOR: *Britton & Millspaugh 5696* (F, NY). LONG ISLAND: *Brace 4230* (F, NY, US). South Clarence Town, *Hill 2289* (MO). NEW PROVIDENCE: Lake Cunningham, *Britton & Brace 640* (F, NY). *Cooper s.n.* (NY). Ca. 1 mi S of Foxhill, *Correll & Popenoe 40321* (MO). Nassau, *Degener 18789* (GH, NY); *Hitchcock s.n.* (F, US); *Meriläinen & Roe 36* (WIS). NORTH CAICOS: Vic. of Kew, *Millspaugh & Millspaugh 9132* (F, NY); *Proctor 9032* (IJ). ROSE ISLAND: Scrub Island, *Britton & Millspaugh 2130* (F, NY, US). RUM CAY: Sclater's Tract, *Brace 3978* (F, NY). SOUTH BIMINI: *Howard & Howard 10069* (GH, NY). WATLING'S ISLAND: *Wilson 7309* (F, GH, NY).

BELIZE. BELIZE: Vic. of Maskall River, *Croat 23924* (MO). Vic. of San José Mayan Indian Village, *Croat 24420* (MO). Gracie Rock, *Dwyer 10971* (MO). 1.5 mi W of Maskall, *O'Neill 8457* (F, GH, UC). Near Manatee Lagoon, *Peck 93* (GH). Rd. to Sibun River, *Rose Innes 58* (IJ, ISC). CAYO: Vic. of Millionario, *Croat 23649* (MO), *23707* (MO). Vaca, *Gentle 2332* (F, GH, US). El Cayo, *Lundell 6145* (F, GH, NY, US); *Lundell 6430* (F, GH, NY, US). COROZAL: Port Sal, *Gentle 103* (F); *Lundell 4904* (NY). ORANGE WALK: Mi 54, Northern Hwy., *Dwyer & Liesner 12209* (MO). Hillbank Camp, *Pelley 33* (F). STANN CREEK: 5 mi S of Lynam Agric. College, *Crankshaw 16* (MO). Carib Reserve, *Gentle 3001* (GH, US), *7975* (F, IJ, NY, UC, US). Broken Ridge, *Gentle 8215* (F, IJ, NY, UC, US). Cohune Ridge, *Gentle 8523* (F, IJ, UC, US). Stann Creek Valley, *Gentle 9089* (US). Middlesex, *Schipp 332* (F, GH, MO, NY, UC, US). Ca. 5 mi S of Lynam Agric. College, *Spellman 1598* (MO). Silkgrass Creek Reserve, *Stevenson 171* (F). TOLEDO: Columbia Forest Station, *Dwyer 9957* (MO). San José, *Dwyer 11155* (MO). Monkey River, *Gentle 3657* (F, GH, MO, NY, US). Near Jacinto Creek, *Gentle 5572* (F, IJ, US). Chavarrias Rd., *Gentle 6278* (IJ, US). Between Machaca and Camp Z, *Gentle 6931* (F, IJ, NY, UC, US). El Dorado Rd., *Gentle 6963* (F, IJ, NY, UC, US). Near Colombia, *Gentle 7098* (US). Near San Antonio, *Gentle 7785* (IJ, US). DISTRICT UNKNOWN: 4 mi W of Salt Marsh, *O'Neill 8492* (F, GH, UC).

CAYMAN ISLANDS. CAYMAN BRAC: *Millspaugh 1172* (F), *1226* (F, US); *Proctor 28962* (IJ). GRAND CAYMAN: *Brandt 1694* (IJ), *2031* (IJ). Governor's Island, *Kings GC166* (MO, NY). Georgetown, *Lewis s.n.* (IJ). LITTLE CAYMAN: *Kings LC94* (MO, NY). SWAN ISLANDS: *Nelson 87* (GH, US); *Proctor 32561* (IJ).

COSTA RICA. ALAJUELA: Vic. of Los Chiles, *Holm & Iltis 728* (A, NY). LIMÓN: Limón area, *Pohl & Calderón 9991* (ISC).

CUBA. CAMAGÜEY: Vic. of La Gloria, *Shafer 23* (F, NY). Cayo Camagüey, *Shafer 2571* (F, GH, NY, P, US). Cayo Coco, *Shafer 2720* (F, GH, NY, US). HABANA: Cerca Managua, *Baker & Wilson 304* (F, NY, US). Anafe, *Ekman 1020* (NY). Cerro de Esperón, *Killip 13509* (US). Vic. of Cojimar, *Killip 13808* (US); *León 1970* (US), *1971* (US). Near Camp Colombia, *León 767* (ISC, US). Vic. Jamaica, *León 2602* (GH, US). Madruga, *León 8945* (GH, NY). Vic. of Jamaica, *León 13658* (GH, US). Almendares River, *Shafer 12464* (US). ISLA DE PINOS: Sierra de los Caballos, *Britton & Wilson 15134* (F, NY). Nueva Gerona, *Curtiss s.n.* (NY). Pedernales Point, *Millspaugh 1422* (F, US). Nueva Gerona,

Palmer & Riley 1001 (NY, US). San Juan, *Roig & Cremata 1779* (NY). LAS VILLAS: Cayamas, *Baker 2501* (F, NY), *4611* (US). Trinidad Mts., *Brues s.n.* (GH, NY). Cienfuegos, *Brues s.n.* (GH); *Combs 148* (F, GH, ISC, MO, NY). Caibarién, *Fernando 349* (GH, US). Sierra de San Juan, *Hodge & Howard 4493* (A). Río San Juan, *Howard et al. 384* (A, ISC, NY, UC, US). Cienfuegos, *Jack 4380* (A, NY, UC). Near Sancti Spiritus, *León 904* (US); *Linden 2* (GH). Loma de Banao, *Luna 26* (NY). Sierra de San Juan, *Morton 4123* (US), *4143* (UC, US). Trinidad Mts., *Morton 4210* (UC, US). Sierra de San Juan, *Morton 4528* (US). Trinidad Mts., *Smith et al. 3269* (F, MO, UC, US). *Webster et al. 206* (A); *Wood & Atchison 7463* (US). MANTANZAS: Mantanzas, *Britton & Wilson 241* (NY). San Miguel de los Baños, *Killip 13919* (US). Near Cauasí, *León 13118* (GH, US). ORIENTE: Guatanomo, *Britton 2106* (NY, US). Santiago, *Clemente 2879* (GH, IJ). Near Playa de Juraguá, *Clemente 7444* (GH, IJ). Near Manatí, *Garteiz 5685* (NY, US). Guatánomo, *Hioram 2198* (NY). Guaro, *Hitchcock 23398A* (US). Sierra de Nipe, *León 20350* (GH). Canamova, *León 21097* (GH). Central Palma, *Linder 5* (GH). Santiago, *Millspaugh 1015* (F, US). Sierra de Nipe, *Morton & Acuna 2914* (GH, MO, NY, US), *3218* (MO, US). Sierra Maestra, *Morton & Acuna 3433* (F, GH, NY, US). Sierra de Nipe, *Morton et al. 8753* (US). Puntón de Cuerro, *Morton & Alain 8879* (US). Vic. of Baracoa, *Pollard et al. 76* (F, GH, MO, NY, UC, US). S of Holguin, *Shafer 1375* (NY, US). Sierra de Nipe, *Shafer 3017* (F, NY, US). Río Yamuri, *Shafer 7827* (NY, US). Farallon de la Perla, *Shafer 8751* (NY, US). Baracoa, *León & Victorin 17336* (GH, US). Santiago, *Taylor 324* (NY); *Underwood & Earle 1642* (NY). 8 km S of Moa, *Webster 3822* (GH, US). 3 km N of El Morro, *Webster 4058* (GH, US). 5 km S of San Pablo de Yao, *Webster 4076* (GH, US). PINAR DEL RÍO: Cajálbana, *Alain 1671* (GH, IJ). Vic. of Pinar del Río, *Britton 10042* (NY). San Diego de los Baños, *León 4662* (US). Rosario Mts., *León 12776* (GH). El Rosario, *León 14118* (US). Vic. of Mendoza, *Shafer 10597* (F, GH, MO, NY). Sierra Mendoza, *Shafer 11149* (F, NY, US). Arroyo del Sumidero, *Shafer & León 13564* (F, NY). Sierra de Anafe, *Wilson 11363* (F, NY, US).

DOMINICAN REPUBLIC. BARAHONA: Barahona, *Abbott 1542* (GH, US). Polo, *Abbott 1840* (GH, US), *1876* (GH, US). Maniel Viejo, *Abbott 1914* (F, GH, MO, US). 12 km NNE of Polo, *Davidse 2721* (ISC, MO). Near Rincón, *Fuertes 1276* (GOET, M), *1476* (GH, MO, US). DISTRITO NACIONAL: Vic. of Ciudad Trujillo, *Allard 13463* (A, US), *13464* (A, MO, NY, US), *13573* (US), *14126* (NY, US), *15750* (US), *18929* (US). Km 32 Santiago-Santo Domingo Hwy., *Davidse 2619* (ISC, MO). Santo Domingo, *Rose et al. 4142* (US). EL SEIBO: E of Jovero, *Abbott 2859* (GH, NY, US). LA VEGA: Cotuy, *Abbott 737A* (IJ, US). Vic. of Piedra Blanca, *Allard 13613* (US). Vic. of Jarabacoa, *Augusto 1015* (NY). 17–18 km N of Jarabacoa, *Davidse 2633* (ISC, MO), *2641* (ISC, MO). Near Hotel Montaña, *Gould & Jiménez 14102* (MO). Vic. of Jarabacoa, *Jiménez 5937* (NY). La Vega to Jarabacoa, *Liogier 12410* (NY). 4 mi S of La Vega, *Liogier 15871* (NY). MACORIS: 23 km W of San Pedro de Macoris, *Howard & Howard 9503* (GH, NY, US); *Rose et al. 4159* (US), *4441* (US). Consuelo, *Taylor 242* (NY). PEDERNALES: 10 mi NE of Cabo Rojo, *Liogier 16944* (NY). PUERTO PLATA: 9 km SW of Sabaneto de Yásica, *Davidse 2674* (ISC, MO). Yaroa, *Jiménez 2764* (US). Loma del Puerto, *Liogier 15917* (NY). SAMANÁ: Vic. of Sánchez, *Abbott 171* (US), *179* (IJ, US). Vic. of Laguna, *Abbott 297* (IJ, US). Vic. of Samaná, *Abbott 506* (IJ, US), *1523* (GH, US). Vic. of Sánchez, *Abbott 1527* (F, GH, US); *Taylor 2* (F, NY). SAN JUAN: El Cerado, *Howard & Howard 8672* (GH, MO, NY, P). SANTIAGO: Navarette, *Abbott 1084* (US). Pico Diego de Ocampo, *Jiménez 1464* (US). Jaiqui to Picado, *Liogier 17049* (NY).

GUATEMALA. ALTA VERAPAZ: Near Finca Sepacnite, *Cook & Griggs 138* (US). Chamá, *Johnson 177* (US). Trece Aguas, *Lewton 286* (US). Cubilquitz, *Standley 70615* (F, US); *von Tuerckheim 7696* (US). ESCUINTLA: Near Escuintla, *Standley 63909* (F). IZABAL: Los Amates, *Blake 7721* (US), *7759* (US). Ca. 7 mi S of Puerto Barrios, *Croat 41779* (MO). Near Puerto Barrios, *Standley 24888* (US), *24889* (F), *25065* (F), *72832* (F, US), *72889* (F). Cerro San Gil, *Steyermark 41967* (F, US). PETÉN: La Libertad, *Aguilar 19* (GH, MO, US). Dolores area, *Contreras 2448* (US), *2591* (US), *2732* (US), *2921* (US), *3043* (GH, IJ, US), *3162* (US). Lacandón, *Contreras 3298* (GH, US). Lake Yaxha, *Dwyer 11239* (MO). La Libertad, *Lundell 1587* (NY, US). Monte Santa Teresa, *Lundell 2734* (US). La Libertad, *Lundell 3548* (US), *4882* (US). Entre Sta. Elena y San Francisco, *Molina 15628* (US). QUEZALTENANGO: El Palmar, *Kellerman 6264* (US). Above Mujuliá, *Standley 85472* (F, US). SANTA ROSA: Near Cuilapa, *Standley 77697* (F).

HAITI. GONAVE ISLAND: Vic. of Anse Galette, *Leonard 3071* (US), *3072* (F, GH, US), *3074* (IJ), *3081* (NY, US). Vic. of Etroite, *Leonard 3293* (US). Vic. of Pikmi, *Leonard 5111* (GH, IJ, US), *5211* (IJ, NY, US). L'ARTIBONITE: Hinche to Papaye, *Anderson 1322* (MO,

UC, US). Vic. of St. Marc, *Leonard 2907* (GH, IJ, NY, US). Vic. of Ennery, *Leonard 8997* (US), *9007* (P, US). L'OUEST: Pétionville, *Ekman 2334* (A, US). Thomazeau, *Ekman 8559* (A, US). Vic. of Port-au-Prince, *Hitchock 19888* (US). Vic. of Mission, *Leonard 3758* (GH, US), *3785* (IJ, US). Pétionville, *Leonard 4848* (GH, IJ, US), *4970* (US). Vic. of Port-au-Prince, *Leonard 5270* (GH, NY, US). NORD: Near Port Margot, *Bartlett 17404* (A, US). Milot, *Buck 471* (GH). Vic. of Marmelade, *Buck 1090* (GH, IJ). La Victoria, *Holdrige 1737* (NY, US). Vic. of St. Michel de l'Atalaye, *Leonard 7011* (IJ, NY, US), *7292* (UC, US), *7605* (F, GH, US), *8052* (MO, US). Vic. of Marmelade, *Leonard 8249* (US). Port de Paix, *Leonard & Leonard 11116* (GH, P, US). Near Port Margot, *Nash 362* (F, NY). NORD-OUEST: Tortue Island, *Leonard & Leonard 11235* (IJ, MO, UC, US), *11352* (US), *11688* (US), *11692* (US), *12539* (NY, US), *15297* (US). SUD: Cayaba to Moron, *Bartlett 17312* (A, UC, US). N of Morne Jeffrod, *Bartlett 17558* (US). Morne Quinille, *Christ 1898* (US). Grande Cayenite, *Eyerdam 326* (GH, MO, P, US).

HONDURAS. ATLANTIDA: Isla de Roatán, *Barkley & Barkley 39669* (MO). 28 km NE of El Progreso, *Davidse & Pohl 2174* (ISC, MO). 33 km SE of Tela, *Davidse & Pohl 2189* (ISC, MO). 17 km SSE of La Ceiba, *Davidse & Pohl 2196* (ISC, MO). Isla Roatán, *Harmon & Dwyer 3962* (MO). Between Saladite and San Francisco, *Molina 20845* (F, NY). Vic. of San Alejo, *Standley 7712* (F). Near Tela, *Standley 53092* (A, F, US), *54282* (A, F, US), *54545* (A, F, US). San Juan Carib Village, *Yuncker 4811* (F, MO, UC). COMAYAGUA: San José de Comayagua, *Davidse & Pohl 2226* (ISC, MO). Near Siguatepeque, *Yuncker et al. 5651* (F, GH, MO, US). Above El Achote, *Yuncker et al. 6012* (F, GH, NY, US). COPÁN: 11 mi S of Chiquila, *Croat 42537* (MO). Entre El Portillo y San Juan Opoa, *Molina 12888* (US). OLANCHO: 3 km SW of Dulce Nombre de Culmí, *Davidse & Pohl 2440* (ISC, MO). Near El Ploma, *Molina 13291* (US).

JAMAICA. CLARENDON: Portland Ridge, *Barry s.n.* (IJ). Lower Clarendon, *Harris 12725* (F, GH, MO, NY, US), *12740* (F, GH, MO, NY, US). Peckham Woods, *Harris 12768* (MO). Portland Ridge, *Lewis s.n.* (IJ). Peckham Woods, *Patrick 118* (IJ). Mason River Savanna, *Proctor 16228* (IJ). W slope of Crofts Mtn., *Proctor 29244* (IJ). Portland Point, *Taylor s.n.* (IJ). Portland Ridge, *Webster 5120* (A). MANCHESTER: Vic. of Mandeville, *Britton 966* (NY); *Brown 136* (NY). Southern Manchester, *Harris 12691* (F, GH, MO, NY, US); *Hitchcock 9838* (US). Sommerset Woods, *Howard & Proctor 14899* (A). PORTLAND: Hope Bay, *Adams 5551* (M). Rodney Hall, *Adams 11638* (MO). Navy Island, *Millspaugh 1820* (F). Between Drapers and Frenchman's Cove, *Wedderburn 198* (IJ). ST. ANDREW: Mona, *Barry s.n.* (IJ). Cooper's Hill, *Crosby & Anderson 1099* (F, MO, NY, UC). Castleton, *Harris 11297* (F, GH, IJ, MO, NY, P, US). Bryan's Hill, *Harris 11528* (F, NY, US), *11530* (NY, US). Vic. of Constant Spring, *Hitchcock 9264* (US), *9267* (US), *9268* (US). Ferry Hill, *Stearn 819* (A). Long Mtn., *Webster 4998* (A, IJ). Long Mtn., *Yuncker 17332* (F, MO). ST. ANN: Between Alderton and York Castle, *Anderson & Sternberg 3086* (US). 1.4 mi S of Ocho Rios, *Davidse & Conroy 3274* (ISC, MO). Mt. Diablo, *Hespenheide 967* (GH, MO, US). Edwarton–Moneaque, *Hitchcock 9449* (US). Lydford Post Office, *Howard & Proctor 13492* (A, IJ). Moneaque, *Hunnewell 14112* (GH). Mt. Diablo, *Maxon & Killip 473* (F, GH, P, US); *Ridley 23* (US). ST. CATHERINE: Old Harbour Bay, *Britton & Hollick 1841* (NY). Mt. Diablo, *Hespenheide 1409* (GH, MO, NY, UC, US). Bog Walk to Spanish Town, *Hitchcock 9304* (US). Edwarton to Linstead, *Hitchcock 9420* (US), *9426* (US). Hollymount, *Maxon 10463* (NY, US). Juan de Bolas, *Proctor 7108* (A, IJ, NY). ST. ELIZABETH: Font Hill, *Britton 1510* (NY). Near Malvern, *Dignum 1* (IJ). Near Ipswich, *Harris 12512* (GH, MO, NY, US); *Hitchcock 9628* (US). S of Gutters, *Howard & Proctor 13841* (A, IJ), *14491* (IJ). ST. JAMES: 0.5 mi WNW of Mocho Crossroads, *Hespenheide 1529* (GH). Montego Bay, *Hitchcock 9687* (US). Adelphi, *Powell 5716* (IJ). ST. MARY: Troy, *Harris 12572* (F, GH, MO, NY, US), *12597* (F, GH, MO, NY, US); *Hitchcock 9802* (US). Cabarita Island, *Proctor 7541* (IJ). ST. THOMAS: Windward Road, *Adams 5501* (MO). 2.3 mi E of Eleven Mile Post jct., *Davidse & Conroy 3258* (ISC, MO). 3 mi S of Claremont, *Hitchcock 9519* (US). TRELAWNY: Vic. of Barbecue Bottom, *Patrick 246* (IJ). Windsor Estate, *Patrick 272* (IJ). WESTMORLAND: Glasgow, *Harris 12629* (MO). Savanna La Mar, *Hitchcock 9881* (US). Blauwearie, *Proctor 7315* (IJ), *9315* (IJ). 1.5 mi W of Little London, *Proctor 11207* (IJ).

LEEWARD ISLANDS. ANTIGUA: Sugar Loaf Mtn., *Box 64* (NY, US). Macarthy Valley, *Box 91* (US). *Rose et al. 3392* (GH, NY, US), *3659* (US), *3660* (US). GUADELOUPE: *Duchaissing s.n.* (GOET, US); *Le Gallo 547* (IJ); *Questel 600* (US), *4023* (US); *Stehlé 2607* (US). MARIE GALANTE: Vic. of Pointe de Folle Anse, *Proctor 20298* (IJ). MONTSERRAT:

Shafer 700 (F, NY, US). NEVIS: *Box 172* (US); *Edwards 085 G* (MO). SABA: *Boldingh 2070* (US). ST. EUSTATIUS: *Boldingh 990* (P). ST. KITTS: *Hitchcock 16354* (US).

MEXICO. CHIAPAS: 50 km S of Palenque, *Beetle M-3902* (MO). 15 km WNW of Ocozocoautla, *Breedlove 29030* (MO). Laguna Miramar, *Breedlove 33311* (MO). Jct. of Río Perlas and Río Jataté, *Sohns 1590* (MEX, US). Near Ocosingo, *Ton 3475* (NY). JALISCO: Tequila, *Palmer 362* (F, GH, ISC, MEXU, MO, US). OAXACA: 5 mi N of Palomar, *Croat 40006* (MO). Temazcal, *Sousa 965* (MEXU), *1328* (MEXU). 3 km al E de Sarabia, *Vazquez 1448* (MO). Ubero, *Williams 9468* (F, US). QUINTANA ROO: Consumel Island, *Beetle M-4226* (MO). Tancah, *Swallen 2812* (US). Gozumel Island, *Swallen 2849* (US). SAN LUIS POTOSÍ: Tamazunchale, *Hitchcock & Stanford 7311* (US); *Kenoyer 1018* (F); *Lundell & Lundell 7119* (NY, MEXU, US), *12405* (MEXU, NY, UC, US). Tamasopo, *Pennell 18014* (GH, US). TABASCO: La Palma, *Matuda 3242* (F, GH, MEXU, US). VERACRUZ: 2 mi W of Córdoba, *Ballwinkel & Wunderlin 403* (WIS). 6 mi E of Coatzacoalcos, *Croat 40038* (MO). Near Tantoyuca, *Ervendberg 281* (GH). Córdoba, *Hitchcock 6456* (US). 4 km N of Minatitlán, *King 1057* (US). Km 56 Veracruz to Coatzacoalcos, *Leija & Garza 756* (MEXU). Ciudad Alemán Cosamaloapan, *Martínez-Calderón 1094* (UC). Zacuapan, *Purpus 2905* (F, GH, NY, UC, US). Vic. of Río Tonto, *Santos 2269* (US). YUCATÁN: Izabal, *Gaumer 1032* (F, GH, MEXU, MO, NY, UC, US). Chichankanab, *Gaumer 2144* (F, GH, NY), *2462* (F). Izabal, *Gaumer 2482* (F). Hunucmá, *Miranda 8087* (MEXU). Mérida, *Schott 675* (F, GH, MO, US). Chichen Itza, *Swallen 2410* (US), *2417* (US), *2452* (US), *2465* (MO, US), *2469* (US). Tizimin, *Swallen 2489* (US), *2512* (US), *2520* (US). Uxmal, *Swallen 2625* (US), *2641* (US). Peto, *Swallen 2706* (US).

NICARAGUA. CHONTALES: Vic. of La Libertad, *Standley 8999* (F). ZELAYA: Bilwaskarma, *Davidse & Pohl 2295* (ISC, MO). Bluefields, *Hampe 12-f* (GOET).

PANAMA. CANAL ZONE: Ancón Hill, *Killip 4028* (US). Albrook Air Force Base, *Stimson 5188* (NY, SCZ). COLÓN: 0.7 mi NE of Río Piedras, *Nee & Mori 3649* (MO, WIS).

PUERTO RICO: Río Piedras, *Blomquist 12083* (UC). Mt. Alegrillo, *Britton et al. 2623* (US). Vic. of Guanica, *Britton et al. 4955* (NY, US). Cayo Muertes, *Britton et al. 5006* (F, NY, US). Vic. of Catano, *Britton et al. 6991* (NY, US). Culebra Island, *Britton & Wheeler s.n.* (F, NY). Mayaguez, *Chase 6157* (US). Vic. of Mariaco, *Chase 6192* (US), *6225* (US). Aibonita to Cayey, *Chase 6335* (US). Vic. of San Juan, *Chase 6365* (US). Vic. of Vega Baja, *Chase 6420* (US), *6431* (US). Vic. of Arecibo, *Chase 6443* (US). Between Utado and Adjuntos, *Chase 6462* (US). Vic. of Guanica, *Chase 6521* (US). Coamo, *Chase 6543* (US). Vic. of Arecibo, *Chase 6560* (US). Vic. of Lares, *Chase 6587* (US). Manatí, *Chase 6610* (US). Viques Island, *Chase 6683* (US). Sierra de Luquilla, *Chase 6726* (US). Vic. of San Juan, *Chase 6782* (US). Mayaguez, *Chase 6814* (US). Mariaco, *Duke 7574* (MO), *7581* (MO). Bayaman, *Goll 227* (NY, US). Cuamo, *Goll 699* (NY, US). Mona Island, *Hess 454* (US). Mayaguez, *Holm 26* (F, GH, MO, US). Vic. of Vega Baja, *Liogier 9795* (IJ, NY). Susua, *Liogier 9899* (F, IJ, NY, VEN). Bayaman, *Liogier 10225* (IJ, US), *10254* (IJ, NY, US). Río Piedras, *Otero 255* (GH, MO, US). Mayaguez, *Sintensis 68* (GOET). Cayey, *Sintensis 2318* (F, NY, P, US), *2470* (MO, US). Mona Island, *Stevens 6337* (NY). Yauco, *Vélez 340* (NY).

UNITED STATES. FLORIDA: BREVARD CO.: Okeechobee Region, *Fredholm 5532* (GH, NY, US). COLLIER CO.: 1 mi NW of Paolita Station, *Ward & Beckner 5345* (GH, NY, US). DADE CO.: Miami, *Chase 3904* (US). Long Pine Key, *Cooley et al. 9197* (GH). Near Miami, *Correll 5974* (GH, US). 15 mi SW of Royal Palm Park Inn, *Deam 60320* (UC). Snapper Hammock, *Eaton 315* (F, GH, US). Tallahassee Hammock, *Eaton 418* (US). Miami, *Hitchcock s.n.* (US). 25 mi W of Miami, *Moldenke 3747* (NY). Biscayne Bay, *Palmer 630* (GH, MO, US). Royal Palm Hammock, *Palmer 27483* (A, MO). Miami, *Rehder 805* (A); *Rolfs & Quaintance 935* (US); *Small & Carter 64* (NY). Between Miami and Coconut Grove, *Small & Carter 561* (F, NY); *Small & Small 4624* (NY), *4647* (GH). Long Key, *Small 7345* (ISC, NY), *s.n.* (UC). Elliott's Key, *Small & Nash s.n.* (NY); *Tracy 9050* (F, GH, MO, NY). Miami, *Tracy 9320* (F, GH, MO, NY). MONROE CO.: Key West, *Blodget s.n.* (GH, US). Key Largo, *Brass 21136* (GH); *Chase 3930* (US); *Correll et al. 40304* (MO). Key West, *Garber s.n.* (NY, US). Big Pine Key, *Killip 32037* (GH, UC, US), *42259* (US); *Martin 1281* (NY, UC, US). Key Largo, *McFarlin s.n.* (NY); *Moldenke 407* (F, MO, NY, P, US). No Name Key, *Muenscher & Thorne 18131* (GH, UC). Key Largo, *O'Neill s.n.* (US). Stock Island, *Pennell 9621* (US). Key Largo, *Pollard et al. 157* (F, NY, US). Key West, *Porter s.n.* (F). Bear Lake Rd., *Robertson 257* (GH). Key West, *Rugel 111* (F, GH, M, NY, US). Big Pine Key, *Siebert 1290* (MO). Tibisee, *Silveus 5270* (US). Big Pine Key, *Simpson 337* (NY). Vaca Key, *Small & Carter 2864* (NY, US). Boca Chica Key, *Small 3947* (NY).

Sugar Loaf Key, *Swallen 5161* (US). Key Vaca, *Swallen 5200* (US). Near Flamingo, *Swallen 5248* (US). Big Pine Key, *Swallen 10668* (US), *10694* (US). 4 mi W of Dade-Monroe Co. line, *Ward & Burch 3306* (US). Stock Island, *Wilbur & Webster 2556* (GH, NY, US). PALM BEACH CO.: Near Palm Beach, *Curtiss 5530* (GH, MO, NY, P, UC, US); *Hitchcock 2547* (US); *Small 2133* (NY); *Webber 204* (MO, NY). ST. LUCIE CO.: S of Fort Pierce, *Small 8771* (NY).

VENEZUELA. ARAGUA: 16.3 km NW of Rancho Grande, *Davidse 3114* (ISC, MO). DISTRITO FEDERAL: Carayaca, *Jahn 312* (US, VEN), *321* (US, VEN). Sosa, *Tamayo 561* (VEN). LARA: Between Terepaima and Cabudare, *Steyermark et al. 103639* (VEN).

VIRGIN ISLANDS: ANEGADA: *D'Arcy 4843* (MO). ST. CROIX: *Raunkiaer 642* (P). Caanon, *Ricksecker 257* (F, GH, MO, NY, P, UC, US), *400B* (F, MO, US); *Rose et al. 3609* (GH, NY, US). *Thompson 385* (US), *430* (GH), *501* (US), *526* (US). ST. JOHN: *Eggers 3058* (M), *3121* (US). ST. THOMAS: *Biédle s.n.* (P). Water Island, *Britton et al. 141* (NY, US). *Eggers 77* (GOET, MO, P), *189* (US), *292* (US); *Hitchcock 16309* (US). Water Island, *Millspaugh 519* (F, NY, US). TORTOLA: Sage Mtn. Ridge, *D'Arcy 2075* (A). *Fishlock 240* (GH, NY); *Shafer 1142* (F, US).

WINDWARD ISLANDS. BARBADOS: Applewhaite's Gulley, *Dash 414* (NY). DOMINICA: *Beard 1370* (F, GH, US); *Hitchcock 16422* (US); *Imray s.n.* (GOET); *Smith & Smith 1105* (NY); *Smith 10306* (US). GRENADA: La Pastoria, *Broadway s.n.* (F, GH, NY, US). St. Davids, *Broadway s.n.* (M, MO). St. Mark Parish, *Proctor 17221* (A). MARTINIQUE: *Hahn 480* (P, UC); *Hitchcock 16458* (US); *Husnot 94* (US); *Stehlé 2086* (US), *4589* (IJ). ST. LUCIA: *Hitchcock 16496* (US); *Smith 10200* (US). ST. VINCENT: *Beard 1370* (MO); *Morton 4724* (US).

2b. **Lasiacis divaricata** (L.) Hitchc. var. **austroamericana** Davidse, Ann. Missouri Bot. Gard. 64: 374. 1978. TYPE: Brazil, Minas Gerais, near Santa Barbara do Caparaco, streamside, suffrutescent, 3 m high, climbing and rooting at lower joints, "canaviera," 21 Nov. 1929, *Mexia 4007* (NY, holotype; F, GH, MO, UC, US, isotypes).

Perennial; culms caespitose, 1–5 m tall, erect at the base, arching and scandent; internodes lignified, to 12 mm wide, hollow, glabrous or with a line of puberulence; nodes glabrous; sheaths usually glabrous, occasionally with a few scattered, delicate hairs near the apex, rarely puberulent throughout, the upper margin ciliate, the auricular hairs to 3 mm long; collar usually glabrous, rarely sparsely minutely puberulent or with a few scattered small hairs; ligule a whitish membrane 0.3–1.2 mm long, glabrous or ciliolate; blades narrowly lanceolate, 5–11(–14) cm long, 0.6–1.8(–3.0) cm wide, usually glabrous, occasionally with a few scattered hairs at the base of the upper and lower surfaces, rarely puberulent throughout, the base asymmetrical, rarely with a few cilia, the margin scabrid, the apex acute to acuminate; panicles small, 2–10(–14) cm long, the longest branch 1–4(–7) cm long, the branches ascending to spreading somewhat at maturity, scabrous and/or puberulent, the pulvini usually puberulent, occasionally glabrous; spikelets globose, 3.4–4.3 mm long, purple or green when immature; first glume (1.5–)1.7–2.4(–2.7) mm long, 7–11-nerved; second glume 9–13-nerved; sterile floret without or with a staminate flower, the anthers 1.7 mm long, the lemma 9–13-nerved, the palea ½ to equal the length of the fertile floret; fertile floret 3.3–3.7 mm long, 2.1–2.3 mm wide, the anthers ca. 2 mm long; caryopsis 2.3 mm long, 1.8–1.9 mm wide; chromosome number $n = 18$.

Ecology: This variety is found along brushy forest edges and in secondary forests. Elevation records range from 100 m to 1,700 m. Spikelet-bearing plants were primarily collected from November through May.

Distribution: *Lasiacis divaricata* var. *austroamericana* is known in Colombia and Brazil south through Peru, Bolivia, Paraguay, and northern Argentina.

Lasiacis divaricata var. *austroamericana* is characterized by its small, narrow, essentially glabrous leaves, small ligule, small panicles with ascending or slightly spreading branches, and globose, short-pedicelled spikelets. Although the overall aspect is glabrous, it is not uncommon to find a few scattered hairs near the base of the leaf blades along the midvein and on the upper part of the sheath.

This variety differs from *L. divaricata* var. *divaricata* in having ascending rather than reflexed panicle branches. This plus the globose spikelets easily differentiate the two. In addition, the leaves of var. *austroamericana* are more lax and not as strictly distichously arranged, and the branches are not or very little zigzag. In all these characters, var. *austroamericana* varies in the direction of *L. sorghoidea* var. *patentiflora* and the glabrous small-spikelet form of *L. nigra*. Parodi (1943) also noted this relationship stating that "esta especies es muy afin a *L. sorghoidea*." However, he did not consider the South American element of *L. divaricata* to be distinct from the Caribbean element.

ARGENTINA. MISIONES: Km 45 El Dorado, *Bertoni 982* (NY). Acaraque, *Bertoni 3100* (US). San José de Pindapoy, *Bridaralli 2625* (F). Parque Iguazú, *Del Puerto & Bescia 2663* (US); *Ekman 616* (US). Loreto, *Ekman 618* (US). 10 km de Cerro Azul, *Krapovickas et al. 15042* (WIS). Santa Ana, *Montes 1736* (F, US). Candelaria, *Montes 2221* (F, US). Feyucuare, *Montes 14802* (MO). Loreto, *Montes 27498* (MO). Colonia Roca, *Mutinelli 50* (US). Puerto Maní, *Schwarz 10232* (US, WIS).

BOLIVIA. BENI: E of Puerto Sucre, *Chase 11152* (US). COCHAMBA: Prov. Chapáre, *Steinbach 9091* (F, GH, GOET, MO, NY, US). LA PAZ: San Carlos, *Buchtien 22* (NY, US). Colaya, *Mexia 4307* (GH, MO, UC). Lower Cocas, *Williams 954* (NY). DEPARTMENT UNKNOWN: Mychariapu River, *Williams 962* (NY).

BRAZIL. CEARÁ: Crato, *Swallen 4356* (RB, US). ESPIRITO SANTO: Santa Teresa, *Sucre & Braga 4565* (MO). MARANHÃO: Ilha de Balsas Region, *Eiten & Eiten 4736* (NY). Barra do Corda to Grajahú, *Swallen 3773* (US). Grajahú to Porto Franco, *Swallen 3788* (US). MINAS GERAIS: 15 km N of Montalvânia, *Anderson et al. 37186* (MO). Juiz de Fóra, *Chase 8619* (F, GH, MO, NY, US). Visçosa, *Chase 9437* (F, GH, ISC, MO, NY, US). Caparo, *Chase 9644* (F, GH, MO, NY). São João del Rey, *Com. Geol. Geogr. 268* (US). Visçosa, *Irwin 2685* (F, NY, UC). Santa Barbara do Caparaó, *Mexia 4007* (F, GH, MO, NY, UC, US). PARANÁ: Itarare, *Dusén 9643* (MO, US). Morungava, *Dusén 16486* (F, GH, MO, UC). Salto Iguassu, *Rambo 53628* (US). 7 km E of Londrina, *Swallen 8733* (US). Campo Morão, Estevao, *Swallen 8959* (US). RIO GRANDE DO SUL: Pilveira Martins, *Lindman 1239.5* (US). Mun. de Montenegro, *Orth 2719* (MO, US). Lindha Bonita pr. Montenegro, *Rambo 40005* (MO, US). Pôrto Alegre, *Reineck s.n.* (GH). RIO DE JANEIRO: Petrópolis, *Chase 12168* (US). Alto Macahé, *Glaziou 17397*(NY, P). Corcovado, *Glaziou 20574* (P, RB, US); *Guillemin 739* (P). Petrópolis, *Jaes & Sionisio 127* (RB). Rio Bom Fim, *Soderstrom 1927A* (MO). Petrópolis, *Sucre & Braga 2752* (MO), *2763* (MO), *4505* (MO). SANTA CATARINA: Herval, *Dusén 11877* (GH). Ibirama, *Klein 2026* (UC). Morro Costa da Lagoa, *Klein 7201* (US). Nova Teutonia, *Planmann 312* (RB). Itapiranga, *Reitz 3775* (NY, UC, US). Alta Matador, *Reitz & Klein 7079* (NY). 9 km W of Popi, *Smith et al. 11783* (NY, UC, US). SÃO PAULO: Ca. 38 km SW of Jacupiranga, *Davidse et al. 10948* (ISC, MO, SP). Butantan, *Gehrt 2641* (US). Cantareira, *Hoehne 3974* (US). Parque do Estado, *Hoehne 29972* (F, NY). São Paulo, *Pickel 5804* (IPA, US). Butantan, *Usteri 9796* (US). Jaragua, *Usteri 9899* (US).

COLOMBIA. BOYACA: *Lawrance 219* (F, GH, MO, NY, US). MAGDALENA: San Andres de Sierra, *Pittier 1650* (US). SANTANDER: Between Suratá and California, *Killip & Smith 16794* (A, GH, NY, US).

PARAGUAY. Santa Bárbara, *Balansa 40a* (P). Puerto Franco, *Bertoni 1342* (NY). Vic. of Caaguazú, *Hassler 8920* (GH, NY). Sierra de Amambay, *Hassler 12087* (US). Near Villarriaca, *Jörgensen 3559* (F, MO, NY, US). Nacunday, *Montes 10926* (US). Sierra de Amambay, *Rojas 9864* (US).

PERU. CUSCO: Urubamba Valley, *Cook & Gilbert 923* (US). Machupicchu, *Vargas 2188*

(US). JUNÍN: Ereñas, *Killip & Smith 25615* (F, NY, US). DEPARTMENT UNKNOWN: Callacate, *Jelski 583* (US).

2c. **Lasiacis divaricata** (L.) Hitchc. var. **leptostachya** (Hitchc.) Davidse, Ann. Missouri Bot. Gard. 64: 375. 1978.

Lasiacis leptostachya Hitchc., Contr. U.S. Natl. Herb. 22: 19. 1920. TYPE: Nicaragua, Jinotepe, jungle, 500 m, stout central canes, branches more or less whorled and slender, floral branches conspicuously flexous, panicles all small, 7 Nov. 1911, *Hitchcock 8718* (US, holotype).

Plants perennial; culms caespitose, 2–5 m tall, erect at the base, arching and clambering into vegetation, the secondary branches 1 per node or fascicled, often zigzag; internodes of the main culms 3–8 mm thick, hollow to almost completely solid with pith, glabrous, or completely and densely appressed papillose-pubescent, with hairs to 1.5 mm long, deciduous in age leaving a roughened main culm, the internodes of branchlets usually glabrous or with a line of puberulence on one side, often completely or partially solid; nodes glabrous or rarely puberulent; sheath glabrous, the margins glabrous or the overlapping margin ciliate with hairs to 2.5 mm long, the auricular hairs to 3.5 mm; collar minutely puberulent or densely pubescent with hairs to 1.3 mm long; ligule membranous, 0.4–0.8(–1.3) mm long, tan, ciliate with hairs to 1.2 mm long; blades linear-lanceolate, 5–10 cm long, 0.4–1.1(–1.6) cm wide, usually completely glabrous, rarely minutely puberulent, the base asymmetrical, the margin scabrid, the apex acuminate; panicles small, the base usually included in the sheath, 1–7(–12) cm long, the longest branch 0.5–4.0 cm long, the branches glabrous, scabrous, or slightly puberulent, short, strictly ascending and appressed, diverging only in age, the pedicels then divergent, the pulvini puberulent below or glabrous; spikelets oblong, 4.2–5.0 mm long; first glume 1.7–2.4 mm long, 7–11-nerved; second glume 9–11-nerved; sterile floret with or without a staminate flower, the anthers 2.2 mm long, the lemma 9–11-nerved, the palea ½ to equal the length of the fertile floret; fertile floret 4.0–4.7 mm long, 1.8–1.9 mm wide, dark brown, the anthers 2.3–2.7 mm long; caryopsis 2.6 mm long, 1.5 mm wide.

Ecology: *Lasiacis divaricata* var. *leptostachya is* found along forest margins and brushy thickets of quebradas and in secondary vegetation up to 1,100 m. It has been collected from October to May.

Distribution: This variety is known from Oaxaca and Chiapas in Mexico, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, and Panama.

This taxon was known for many years only from the type specimen and in recent years has been confused with narrow-leaved Mexican and South American specimens of *L. nigra*. Its close relationship to *L. divaricata* var. *divaricata* has not been noted before, probably because the type was based on a specimen with papillose-pubescent culms, a character unknown in var. *divaricata*. A hint at the close relationship between *L. leptostachya* and *L. divaricata* was, however, made by Hitchcock through notations on his Nicaraguan collections. On two of these (*Hitchcock 8722, 8723*), he noted "=8718," the holotype of *L. leptostachya*. However, these two specimens were also annotated as *L. divaricata*

and so cited by him (Hitchcock, 1920). Variety *leptostachya* is similar to var. *divaricata* in having small, narrow, usually glabrous leaves, and inflorescences with finally reflexed panicle branches and divaricate pedicels. Since the panicles are partially included in the sheaths, they do not show the characteristic *divaricata* branching pattern until they are quite mature, and most herbarium specimens of this variety show only compact immature inflorescences. The spikelets tend to be less obovate than in var. *divaricata* and somewhat larger, but they resemble the spikelets of this species more than any other taxon. Variety *leptostachya* differs from var. *divaricata* in its narrower leaves, occasionally heavily pubescent culms, somewhat larger and more oblong spikelets, panicles usually partially included in the upper sheaths, and more densely arranged spikelets. Variety *divaricata* can best be distinguished from narrow-leaved, glabrate plants of var. *leptostachya* by the more open, exserted panicles.

All specimens but one bear small secondary panicles only. In *Rodríguez 1352* from Morazán, Honduras (F), one branch shows a distinctly larger terminal inflorescence.

COSTA RICA. ALAJUELA: El Rodeo, *Hunnewell 16552* (GH). GUANACASTE: Between Colonia Carmona and Buena Vista, *Jiménez 378* (US). Santa Rosa National Park, *Liesner 4229* (MO). Matambu, Nicoya, *Tonduz 13748* (P, US). SAN JOSÉ: Llano Grande de Puriscal, *Jiménez 892* (US).

EL SALVADOR. Vic. of San Salvador, *Calderón 508* (GH, NY, US). *Renson 323* (US). Vic. of Ahuachapán, *Standley & Padillo 2498* (F). Vic. of San Salvador, *Standley 19136* (GH, US). Vic. of Ahuachapán, *Standley 19878* (GH, MO, US).

GUATEMALA. CHIQUIMULA: Above El Rincón, *Standley 74696* (F, US). ESCUINTLA: Near Las Lajas, *Standley 58154* (F). JALAPA: Guastatoya, *Kellerman 7847* (F, NY). JUTIAPA: Vic. of Jutiapa, *Standley 74992A* (F), *75416* (F, US). SANTA ROSA: SE of Barbabecena, *Standley 77854* (F, US). La Sepultara, *Standley 79364* (F, US). SUCHITEPÉQUEZ: Above Patulul, *Standley 62204* (F, US). DEPARTMENT UNKNOWN: *Bernoulli 48* (NY); *Bernoulli & Cairo 930* (GOET), *951* (GOET).

HONDURAS. EL PARAÍSO: 32 km W of Danlí, *Davidse & Pohl 2145* (MO). LA PAZ: 5 km a Sabanetas, *Molina & Molina 13894* (US). OLANCHO: Rd. to Las Lomas, *Standley 18475* (F). MORAZÁN: Camino San Antonio, *Rodríguez 1352* (F).

MEXICO. CHIAPAS: 6.5 km W of Tuxtla Gutiérrez, *Breedlove 20164* (DS). Above El Chorreadero, *Breedlove & Thorne 20429* (DS). Near Riso de Oro, *Breedlove & Thorne 20697* (DS, MO). 13 km N of Arriaga, *Breedlove 28304* (DS, MO). NE of Jaltenango, *Miranda 6929* (MEXU). OAXACA: 9 mi SE of Tapanatepeque, *Breedlove & Raven 13704* (MEXU, NY).

NICARAGUA. BOACO: Boaco, *Seymour 3840* (F, GH, MO, NY). CARAZO: Jinotepe, *Hitchcock 8722* (US), *8723* (GH, US).

PANAMA. CANAL ZONE: Near Alahuela, *Dodge et al. 16513* (US). 1 mi N of Madden Dam, *Lazor 2945* (MO). Chagres Valley, *Pittier 2342* (GH, NY, US). Madden Lake, *Witherspoon & Witherspoon 8815* (ISC, MO, TAES). DARIÉN: Camp Dubaganala, *Duke 15495* (US).

3a. **Lasiacis grisebachii** (Nash) Hitchc. var. **grisebachii**, Bot. Gaz. (Crawfordsville) 54: 302. 1911.

Panicum grisebachii Nash, Bull. Torrey Bot. Club 35: 301. 1908. TYPE: Cuba, vicinity of Madruga, coral rock ravine, 28 Mar. 1903, *Britton, Britton & Shafer 758* (NY, holotype, fragment US).

Perennial; widely creeping and branching, forming low, dense mats, only the distal ends of the branches erect to 6 dm, rooting at the lower, procumbent nodes, forming long prop roots that remain unbranched above the soil surface;

culms relatively slender, 2–3 mm thick, herbaceous to moderately lignified, hollow but usually with striplike pith remnants which form an interconnecting network; internodes usually glabrous with a single line of puberulence, rarely the entire upper portion puberulent; nodes glabrous; sheaths usually puberulent, sometimes hirsute, rarely minutely puberulent between the nerves and appearing glabrous, the overlapping margin ciliate, the auricular hairs occasionally prominent and to 3.0 mm long; collar usually with a line of puberulence at its base; ligule an inconspicuous membrane, 0.3–0.6 mm long, glabrous, or sometimes minutely ciliolate; blades 6–14 cm long, 0.6–1.1(–1.4) cm wide, narrowly linear-lanceolate, the upper surface usually glabrous, less commonly sparsely puberulent, pubescent, or hirsute, the lower surface usually puberulent, at least at the base, occasionally glabrous, the margin scabrid, the apex acuminate, the base asymmetrical; panicles relatively small, (2–)5–13(–16) cm long, the longest branch 1–5(–7) cm, bearing evenly distributed spikelets throughout, the branches scabrid, the pulvini puberulent or sparingly pubescent at the lowest nodes; spikelets 3.5–3.8 mm long, globose; first glume 1.5–2.2 mm long, 5–7-nerved; second glume 7–11-nerved; sterile floret usually without a flower, sporadically with a rudimentary or fully developed staminate flower, the lemma 7–11-nerved, the palea equal or subequal to the length of the fertile floret; fertile floret 3.0–3.1 mm long, 2.3–2.5 mm wide, often with a sterile projection at its base, the anthers ca. 2.0 mm long.

Ecology: *Lasiacis grisebachii* var. *grisebachii* is primarily a forest species that occurs predominantly at elevations below 1,000 m, although occasional collections are from somewhat higher elevations. It is most often encountered in shade in secondary forest but occurs in undisturbed habitats as well. Spikelet-bearing specimens have been collected from late June to March in Central America and from late October to the middle of March in Cuba.

Distribution: *Lasiacis grisebachii* var. *grisebachii* extends from San Luis Potosí, Oaxaca, Puebla, and Veracruz south throughout the Yucatán Peninsula into Honduras. It is also found in the western half of Cuba.

In designating the type, Nash (1908) provided the following information: "Type specimen collected in the vicinity of Madruga, by Britton & Shafer *no.* 758, March 28, 1903, in the herbarium of the New York Botanical Garden." The label of the type specimen from NY actually states the collectors to be N. L. Britton, E. G. Britton, & J. A. Shafer, rather than Britton & Shafer as indicated by Nash. This appears to be a simple oversight in citation by Nash since all other information on the label corresponds to Nash's type citation, and I have seen no other specimen at NY which has otherwise identical label information. Hitchcock (1920, 1936) subsequently followed Nash in mistakenly citing *Britton & Shafer 758*.

Lasiacis grisebachii var. *grisebachii* is a relatively uniform taxon characterized by its creeping, hollow stems with pith remnants, short narrow blades, and small inflorescences with globose spikelets. The pith remnants in the culms many times have a distinct greenish tint which differs from the typically white or light tan pith of *L. linearis*, *L. rhizophora*, and *L. oaxacensis*, the three solid-culm

species of *Lasiacis*. The blades have a thick, smooth, dark green appearance that is difficult to describe but quite characteristic to one familiar with the species. A small, sterile projection at the base of the fertile floret is often present. The frequency of this structure is noticeably different in the two floristic regions the species occupies, since it occurred in 96% of the spikelets examined from Mexico and Central America but only in 37% of the Cuban specimens. Although this projection definitely represents the rachilla and floret of a second fertile floret, it is usually reduced to a narrow stalklike structure less than 1 mm long. In only one Cuban collection have I observed it to be more fully developed. On the whole, there is little other regional morphological differentiation of the species.

Poorly collected specimens without the lower, root producing nodes may be mistaken for *L. divaricata*. However, in the latter species, the spikelets are obovate, the panicle branchlets are reflexed at maturity, the culm is more robust and lignified, and the leaf blades are usually relatively shorter and broader than in *L. grisebachii*.

Hitchcock (1936) reported this species from the Oriente province in Cuba on the basis of *León 5685*. This specimen is actually *L. divaricata*. Furthermore, depauperate specimens of *L. divaricata* from Hispaniola have been identified at *L. grisebachii*. I have not seen any authentic specimens of *L. grisebachii* from this island.

BELIZE. BELIZE: Maskall Rd., *Gentle 866* (MO, NY, UC, US). Mi 22 on Western Hwy., *Liesner & Dwyer 1483* (MO). CAYO: Between El Cayo and Benque Viejo, *Bartlett 11505* (US). Vic. of Grano de Oro, *Croat 23334* (MO). Ca. 3 mi S of Grano de Oro, *Croat 23398* (MO). Hummingbird Hwy., *Gentle 8441* (F, IJ, NY, UC, US), *8864* (F, IJ, NY, US). 41 mi Belize-El Cayo Rd., *Gentle 9641* (F, IJ, NY, UC, US). Cohune Ridge, *Lundell 6451* (F, NY, US), *6751* (F, NY, US). Millionario, *Proctor 29866* (IJ). ORANGE WALK: Honey Camp, *Lundell 10* (F), *559* (GH, ISC, MO, NY, US). STANN CREEK: Lynam, *Dwyer et al. 544B* (MO). Hummingbird Hwy., *Gentle 8384* (F, IJ, NY, UC, US). TOLEDO: Río Grande, *Gentle 4798* (F, IJ, US). Edwards Rd. beyond Columbia, *Gentle 6523* (F, US), *6526* (US). Wilson Rd., *Gentle 6849* (F, IJ, NY, UC, US). El Dorado Rd., *Gentle 6965* (F, US). Near Columbia, *Gentle 7101* (F, IJ, ISC, US). Near San Antonio, *Gentle 7523* (F, IJ, NY, UC, US).

CUBA. HABANA: Lomas de Camoa, *Ekman A.G.N.H.794* (F, GH, MO, NY, P, UC). Loma de Coco, *Ekman A.G.N.H.1024* (GH, MO, NY, P, UC, US, WIS). Lomas de Camoa, *Ekman 13531* (F, NY, US); *León 1972* (US). Sierra de Anafe, *León 2874* (GH). La Vigia, Tapaste, *León 10666* (GH, NY, US). Jamaica, Loma de Somorrostro, *León & Roig 11438* (US). MANTANZAS: Santa Clara, Peninsula de Zapata, *Ekman 18340* (US). Mantanzas, *Rugel 187* (GH, GOET, NY). PINAR DEL RÍO: Las Pozas, Pan de Guajaibaí, *Alain 2415* (GH). Taco-Taco, *Baker 3817* (F, NY, US). Guanajay, *Baker & Van Herman 4264* (US). Cabañas, *Ekman 10506* (NY). Gerardo, *Ekman 12646* (US). 30 km N of Pinar del Río, *Hitchcock 23315A* (US). Viñales, *Killip 13528* (US). Sierra del Brujo, *León 12916* (GH, US). Viñales, *León 14715* (GH). Taco-Taco, *Morton 4276* (UC, US), *4306* (F, NY, UC, US), *4390* (GH, MO, US). N of San Cristóbal, *Roig 1183* (NY). Bahía Honda to El Rosario, *Shafer 12006* (F, NY, US). Sierra de Anafe, *Wilson & León 2874* (US). Vic. of Buenaventura, *Wilson 9238* (NY, US). Sierra de Anafe, *Wilson 11309* (F, NY, US); *Wilson & León 11467* (F, NY, US).

GUATEMALA. PETÉN: Vaxactum, *Bartlett 12190* (GH, NY, US). Dos Lagunas, *Contreras 1596* (IJ, US). Dolores, *Contreras 2849* (GH, US). Tikal, *Contreras 3903* (US); *Lundell 16144* (F, US). San Luis, *Lundell 16360* (US). Tikal, *Lundell 16665* (US). Sayaxche, *Lundell 17970* (US). Entre Libertad and Subin, *Molina 15503* (US). Tikal, *Ortíz 326* (F, ISC, MO, NY). Near San Diego, *Steyermark 45305* (F, US). QUEZALTENANGO: Between Finca Pirineos and Patzulín, *Standley 86936* (F, US).

HONDURAS. OLANCHO: 12 km S of Dulce Nombre de Culmí, *Davidse & Pohl 2442* (ISC, MO). SANTA BÁRBARA: Between Lago Yojoa and El Sauce, *Davidse & Pohl 2218* (ISC, MO). Lago Yojoa, *Pohl & Gabel 13410* (MO). Near El Sauce, *Williams & Molina 17986* (F, GH).

MEXICO. CAMPECHE: Monterrey, *Lundell 1243* (F, GH, ISC, NY, UC, US). CHIAPAS: 32 km N of Ocozocoautla, *Breedlove & Raven 13566* (MEXU); *Breedlove 38201* (MO). 32 km NW of Ocozocoautla, *Breedlove 27463* (MO). 6–12 km S of Palenque, *Breedlove 28838* (MO). 13 km N of Berriozábal, *Breedlove & Dressler 29722* (MO). OAXACA: 1 km N of Tolosito, *Pohl & Davidse 11819* (ISC, MO). Jct. of Río Perlas and Río Jataté, *Sohns 935* (MEXU). Tuxtepec, *Sousa 935* (MEXU). PUEBLA: Cerro de Tlaquexpa, *Santos 2594* (ISC, US). Xicotepec de Juárez, *Scheinvar 605* (MEXU). QUINTANA ROO: Laguna Chichan Canab, *Swallen 2750* (MEXU, MO, US). Tancah, *Swallen 2823* (US). SAN LUIS POTOSÍ: Tamasunchale, *Kenoyer 375* (MO). VERACRUZ: Between Martínez de la Torre and Misantla, *Gómez-Pompa & Riba 183* (MEXU). Zongolica, *Santos 2650* (NY), *3734* (NY, US).

3b. **Lasiacis grisebachii** (Nash) Hitchc. var. **lindelieana** Davidse, Ann. Missouri Bot. Gard. 64: 375. 1978. TYPE: Cuba, Habana, Lomas de Camoa, in siloa locis umbrasis satis frequens, 27 Nov. 1921, *Ekman 13530* (US-1295003, holotype; F, NY, US-1502317, isotypes).

Similar to var. *grisebachii* except in the following respects: sheaths puberulent, ciliate on the overlapping margin; collar with a line of puberulence at its base; auricular hairs 1.5–2.0 mm long; ligule a glabrous membrane, 0.5–0.7 mm long, occasionally minutely ciliate; blades linear-lanceolate to lanceolate, 9–14 cm long, 1.5–2.0 cm wide, glabrous on both surfaces; panicles 8–13 cm long, the longest branch 4–7 cm long; spikelets 3.8–4.0 mm long; first glume 1.7–1.8 mm long; sterile palea equal in length to the fertile floret.

Ecology: Variety *lindelieana* is ecologically similar to var. *grisebachii* in being a forest species. Flowering specimens have been collected in November.

Distribution: This variety is known only from Pinar del Río, Habana, and Mantanbas, the three most western provinces in Cuba.

Five Ekman collections from Cuba, including the type of this variety, and one from the Dominican Republic were treated by Hitchcock (1936) as the only West Indian representatives of *L. rhizophora*. I do not concur with Hitchcock's treatment. The Dominican specimen is discussed under *L. rhizophora*. The Cuban specimens have the hollow culms, glabrous blades with essentially nonciliate ligules, globose spikelets with well-developed sterile paleas, and the small inflorescences with evenly distributed spikelets characteristic of *L. grisebachii*. They do differ noticeably from the majority of the representatives of this species in having broad blades (1.5–2.0 cm) which are similar to narrow-leaved specimens of *L. rhizophora*. This is the only resemblance; in all other respects this taxon resembles *L. grisebachii*. Attached to the type specimen on two handwritten labels is the proposal by Ekman for a new name, *L. lindelieana*, as well as the following information:

"Obs. I. Same kind of localities as *L. grisebachii*. To date known from two localities only, Río de Mosquitos in Prov. Pinar del Río and Lomas de Camoa near Habana. Obs. II. Dedicated to my friend Mr. A. R. Lindelie from St. Petersburg, Fla., administrator of San Ramón near Muriel, where I have been living these last two years. Obs. III. Related to *L. grisebachii*, but easily recognized on its broader, smoother, nearly glabrous blades and its more robust nature."

Ekman cooperated closely with Hitchcock in his West Indian botanizing. Since Hitchcock judged the specimens to represent an outlying population of the more southernly distributed *L. rhizophora*, Ekman's name was never published and for many years survived only as a herbarium name. I believe Ekman was correct in recognizing these specimens to represent a new taxonomic entity which is closely related to *L. grisebachii*. Infraspecific, rather than specific status is warranted since the plants differ most notably only in the broad blades. In most other *Lasiacis* species, even such recognition would be difficult to justify. However, the bulk of *L. grisebachii* var. *grisebachii* specimens do have distinctly narrower blades. This gives this broad-bladed group of specimens a very distinctive appearance.

CUBA. HABANA: Lomas de Camoa, *Ekman A.G.N.H.1023* (GH, ISC, MO, NY, P, UC, WIS), *13511* (F, GH, US), *13530* (F, NY, US). Urdagme Hill, near Jamaica, *León 1969* (US). MANTANZAS: Pan de Mantanzas, *Ekman 16464* (US). PINAR DEL RÍO: Mariel, *Ekman 13046* (US). Sierra de los Organos, Grupo del Rosario, *Ekman 17542* (NY, US).

4. **Lasiacis harrisii** Nash, Torreya 13: 274. 1913. TYPE: Jamaica, vicinity of Cinchona, Cinchona to Strawberry Hill, 2–10 Sep. 1906, *Marble 222*. (NY, holotype).

Perennial; culms 1–6 m long, slender, caespitose, erect at the base and arching above, commonly climbing or clambering into surrounding vegetation; internodes of main culms hollow, 2–4 mm thick, glabrous, those of the ultimate branchlets with a line of hairs; nodes glabrous; primary branches usually 1 per node, the secondary and tertiary branches often fascicled with 2 or more per node, the ultimate branchlets slender, hanging down in sprays; sheaths usually glabrous, those of young leaves sometimes sparsely pubescent, these becoming glabrate with maturity, the upper margin ciliate with hairs ca. 1.5 mm long, the auricular hairs few but prominent, to 3.5 mm long; collar glabrous; ligule membranous, 0.4–0.7 mm long, glabrous; blades linear, 6–12 cm long, 0.3–0.7 mm wide, often glabrous, sometimes pubescent at the base and along the midrib, rarely pubescent throughout in young leaves, the base slightly asymmetrical, rarely with a few cilia on the margin, the apex acuminate, the margin scabrid; panicles small and narrow, 2–7 cm long, with short, scabrid, appressed branches, the base included in the upper sheath, the pulvini glabrous; spikelets 3.7–4.0 mm long, first glume 2.0–2.5 mm long, 9-nerved; second glume 9-nerved; sterile floret without a flower, its palea ⅔ to subequal the length of the fertile floret, the lemma 9-nerved; fertile floret 3.2–3.4 mm long, 1.8–1.9 mm wide; caryopsis 2.2 mm long, 1.5 mm wide; chromosome number $n = 18$.

Ecology: *Lasiacis harrisii* grows in moist, montane forests and cloud forests from 800 to 1,500 m. It has been collected from October to November.

Distribution: *Lasiacis harrisii* is endemic to the Blue Mountains of eastern Jamaica.

Lasiacis harrisii is characterized by the relatively long, narrow blades with glabrous collars and small, narrow, partially included panicles with short appressed panicle branches. It is most closely related to *L. divaricata* var. *divaricata*

from which it can be distinguished, in addition to the characters just mentioned, by the tendency to a somewhat larger first glume, by the narrower elliptic spikelet that is not obovate as in *L. divaricata*, and by its relatively straight branches which in *L. divaricata* are usually zigzag.

The distinction between *L. harrisii* and *L. divaricata* var. *divaricata* is not very great, and specific distinction is only maintained with hesitation. There are a number of collections of *L. divaricata* from throughout the West Indies that approach *L. harrisii* vegetatively in having narrow leaves. Most of these collections represent highly branched plants which have proportionally shorter blades than those of *L. harrisii*. This, along with the reflexed or widely spreading branches bearing obovately shaped spikelets, serves to distinguish these *L. divaricata* specimens from true *L. harrisii*.

I differ from Hitchchock (1936) in assigning four Chase collections from Puerto Rico to *L. divaricata* var. *divaricata*. Although these collections resemble Jamaican *L. harrisii* rather closely vegetatively, they differ in having puberulent collars and in having pancile branches which are more divergent and bear more obovately shaped spikelets. In addition, there are other collections from the Dominican Republic, St. Vincent, and Marie Galante which also seem to bridge the gap between *L. harrisii* and *L. divaricata*. These have also been assigned to *L. divaricata*. The number of these intermediate collections is small in proportion to those that are "good" *L. divaricata*, and for this reason, I have maintained these two taxa at the specific level. It would, however, be very valuable to be able to hybridize these two species to determine whether sterility barriers exist. If such studies showed no or only weak barriers, then treating *L. harrisii* at an infraspecific level might better reflect its relationship with *L. divaricata* var. *divaricata*. Observation in the field in Jamaica indicated no overlap between the two species, which seem ecologically rather well separated.

Examination of two Jamaican populations, in addition to the herbarium specimens, failed to turn up plants having larger terminal inflorescences at the end of the main culms. All culms had a few to many small inflorescences on the ultimate branchlets of the culm. In this respect, *L. harrisii* resembles *L. scabrior* which also lacks the large terminal inflorescences so characteristic of all other *Lasiacis* species. The resemblance is further strengthened in that the lower part of the inflorescences of both species are included in the upper sheath.

JAMAICA. PORTLAND: Greenhills to Section, *Adams 9878* (M). Muriel's Rock, *Davidse & Proctor 3242* (MO). Upper Nanny Falls, *Morley & Whitefoord 758* (MO). Between Section and Hardwar Gap, *Proctor 23405* (IJ). ST. ANDREW: Yallah's Bridge below Chestervale, *Davidse & Proctor 3248* (MO). Mt. Faraway, *Harris 11486* (F, IJ, NY). Strawberry Hill, *Harris 11487* (MO, P). Catherine Peak, *Harris 11552* (F, GH, MO, NY, P, US); *Hitchcock 9726* (MO, US), *9730* (US). Chestervale, *Proctor 23834* (IJ). Port Royal Mts., *Proctor 25592* (IJ). ST. THOMAS: Farm Hill, *Orcutt 3544* (MO, US). Vic. of Whitfield Hall, *Proctor 9585* (IJ). PARISH UNKNOWN: Below Cold Spring Gap, *Harris 11354* (NY, US). Abbey Green, *Harris 11587* (F, GH, MO, NY, P, US); *Hitchcock A.G.N.H.588* (F, GH, MO, NY. P, US).

5. **Lasiacis ligulata** Hitchc. & Chase, Contr. U.S. Natl. Herb. 18: 337. 1917. TYPE: Trinidad, near Port of Spain, above St. Anns, among bushes along

stream, high climbing, 28 Nov. 1912, *Hitchcock 10007* (=Amer. Grass Natl. Herb. No. 589) (US-865564, US-865565, holotype; F, GH, MO, NY, isotypes).

Panicum fruticosum Salzm. ex Steud., Syn. Pl. Glum. 1: 74. 1854, pro syn. TYPE: Brazil, Bahia, *Salzmann* (US).

P. megacarpum Steud. in Lechl., Berb. Amer. Austr. 56. 1857, nom. nud. TYPE: Peru, in silvis uliginosis prope San Govan, *Lechler 2219* (GOET, P).

P. divaricatum L. var. *puberulum* Griseb., Fl. Brit. W. Ind. 551. 1864. TYPE: Trinidad, *Mr. Crueger s.n.* (GOET, holotype).

P. divaricatum var. *puberulum* Sodiro, Anales Univ. Centr Ecuador 1889: 5. 1889, nom. nud. non *P. divaricatum* var. *puberulum* Griseb., 1864.

P. maculatum Aubl. var. *pilosa* Fourn., Mex. Pl. 32. 1886. TYPE: Brazil, Bahia, *Salzmann* (P, lectotype).

Perennial; culms 1–5(–10) m tall, caespitose, erect at the base, arching above, the branches solitary or fascicled at the nodes; internodes glabrous or with a line of puberulence on the side, rarely puberulent throughout at the apex, hollow, 6–13 mm thick, lignified; nodes glabrous; sheaths glabrous, puberulent, rarely pubescent, the overlapping sheath margin usually ciliate, rarely completely glabrous; collar sparsely to densely puberulent, or occasionally glabrous; ligule membranous, (1.6–)2.0–3.0(–3.7) mm long, dark brown, sometimes pale, glabrous or appressed pubescent, the margin ciliate with hairs 0.5–2.5 mm long, the apex glabrous or ciliolate with hairs 0.2–0.5 mm long; blades narrowly to broadly lanceolate (5–)7–14(–17) cm long, (0.6–)1.0–2.2(–3.4) cm wide, glabrous or puberulent, the base asymmetrical, rarely ciliate with a few long hairs, the margin scabrid, the apex acuminate; panicles 2–17(–21) cm long, the longest branch 1–8 cm, spikelet density moderate, the panicle branches usually reflexed, or sometimes only widely spreading, glabrous or minutely scabrid above, rarely puberulent, the pulvini usually glabrous, occasionally puberulent; spikelets (3.0–)3.2–3.8(–4.1) mm long, usually purplish when immature; first glume (1.4–)1.7–2.0(–2.3) mm long, 7–11-nerved; second glume 9–11-nerved; sterile floret usually without a flower, rarely with a staminate flower, the lemma 9–11-nerved, the palea ¾ to equal the length of the fertile floret; fertile floret 2.8–3.1(–3.5) mm long, 1.9–2.3 mm wide, dark brown, the anthers 1.6–2.1 mm long; caryopsis 1.8–2.1 mm long, 1.6–1.9 mm wide; chromosome number $n = 18$.

Ecology: *Lasiacis ligulata* is typically found along brushy forest margins, in thickets, in secondary vegetation, along river banks, along roadsides, and in forest openings. The majority of collections are from below 1,000 m but from western South America, elevations of up to 2,100 m have been recorded. In the southern part of its range in South America, spikelet-bearing plants have been collected primarily from March to August. In the northern part and the West Indies, *L. ligulata* has been collected primarily from June to March.

Distribution: *Lasiacis ligulata* occurs from the Dominican Republic south through the West Indies, the Guianas, Brazil, and Bolivia. It is common in Peru but relatively rare in Ecuador, Venezuela, and Colombia.

This species long went unrecognized as a distinct entity, but it is the most common one in the Guianas and Brazil. As Hitchcock & Chase (1917) noted after their description, it is closely related to *L. divaricata* (var. *divaricata* of this treatment). *Lasiacis ligulata* can best be distinguished from the latter taxon

by its longer ligule. The nearly straight, not zigzag, culms, and smaller spikelets that are usually purplish, not green, when immature also distinguish *L. ligulata* from *L. divaricata* var. *divaricata*. The spikelet density in the panicle is also greater than in *L. divaricata*, and the pedicels of *L. ligulata* tend to be shorter and do not diverge as widely at spikelet maturity as those of *L. divaricata* var. *divaricata*. Moreover, puberulence on the lower blade surface is common in *L. ligulata* but quite rare in *L. divaricata*. See also under *L. sorghoidea* for a discussion of intergradation with that species.

The most common form, as described by Hitchcock & Chase (1917), has blades glabrous on the upper surface and on the back of the sheath, whereas the collars and lower blade surfaces are puberulent. This form extends throughout the range of the species but is especially common in the West Indies, the Guianas, and the upper half of Brazil. Also found in Brazil is a form that is completely glabrous, except for some puberulence on the collar. This glabrous form is found in northern Brazil, including Maranhão, Pará, and Amapa and appears again throughout Peru where it is the dominant form. A completely puberulent form is most common in central and southern Brazil from Pernambuco to Mato Grosso and south through the remainder of the southern range of this species.

Common names: Brazil: Pará, taboquinha, *Archer 8254*. West Indies: Tobago, tibisee, *Andrews 610A*.

BOLIVIA. Antochuacorna, 150 km NW of Cochabamba, *Buchtien 2499* (US). 4 km N of Santiago de Chiquitos, *Cutler 7007* (US). Guanai, *Rusby 191* (GH, NY). Head of the Beni River, *White 1004* (NY, US).

BRAZIL. ACRE: Vic. of Campinas, *Forero et al. 6310* (MO). Rio Juruá-Mirim, *Maas et al. P13109* (MO). AMAPÁ: Macapá, *Black & Fróes 51-12282* (US). Serra do Navio, *Cowan & Maguire 38105* (F, NY, RB, US). Tumac Humac, *de Granville 1380* (CAY). Mt. Carupina, *Pires & Westra 48844* (M, NY, US). Near Pôrto Platon, *Pires et al. 51007* (NY, US). Vic. of Igarape Ariramba, *Pires & Cavalcante 52353* (MO, US). Calcoene, *Pires & Cavalcante 52548* (MO, US). Trijonction-Mitaraka, *Sastre 1610* (CAY), *1672* (CAY). AMAZONAS: Manaus, *Chagas 3794* (US); *Ducke 150* (US). Ilha de Bates, Rio Tocantinus, *Pires & Black 2106* (US). Rio Purus, *Prance et al. 13723* (MO). BAHIA: Rodovia Itabuna to Ilhéus, *Belém 1657* (US). Vic. of Bahia, *Chase 8027* (GH, MO, US). Colonia de Gongugy, *Curran 36* (F, GH), *557* (F, GH). Porto Seguro, *Lanna & Castellanos 1484* (MO). Bahia, *Salzmann s.n.* (P-475074). Cruz de Almas, *Santos & Sacco 1921* (US). Near Itabus, *Silva 58356* (US). Ca. 48 km N of Itabebí, *Soderstrom et al. 2132* (MO). Reserva Biológica do Pau Brasil, *Soderstrom et al. 2190* (MO). CEARÁ: Serra de Baturité, *Eugenio 1198* (RB). Assemi, *Sucre & Silva 9257* (RB). DISTRITO FEDERAL: Ca. 25 km N of Brasília, *Irwin et al. 13958* (MO, US). Parque Municipal do Gama, *Irwin et al. 14155* (MO, US); Praia de Sernambetiba, *Smith 6335* (US). Near Guaratiba, *Smith 6510* (US). Country Club, *Sucre 447* (RB, US). ESPIRITO SANTO: Jatiboca, *Brade et al. 18411* (RB). Alegre, *Chase 10048* (US). Espirito Santo. *Kuhlmann 110577* (RB). Near Muqi, *Soderstrom & Sucre 1957* (MO). Reserva de Sooretama, *Sucre 5522* (MO). Vitoria, *Sucre & Araujo 10743* (MO). GOIÁS: Serra Geral do Paraná, *Anderson 7537* (MO). Between Viannapolis and Ponta Funda, *Chase 11321* (F, GH, NY, US). Vic. of Goiás, *Chase 11459* (MO, US). Coyandira, *Chase 11589* (US). Santa Rita do Paranahyba, *Chase 11642* (US). Between Jataly and Rio Araguarja, *Chase 11748* (US). 31 km N of intersection of Hwy. BR-153 and GO-54, *Davidse et al. 12241* (MO). Southern Serra Dourada, *Dawson 15027A* (US). Serra do Morcêgo, *Irwin et al. 15155* (MO). Chapada dos Veadeiros, *Irwin et al. 24186* (MO), *24237* (MO). GUANABARA: Restinga de Grumarin, *Almeida 1313* (MO). Gávea, *Duarte 5221* (MO, RB). Rio de Janeiro, *Plowman & Sucre 2763* (US). Serra da Mendanha, *Soderstrom & Sucre 1948* (MO). Alto da Boa Vista, *Sucre 2098* (MO); *Sucre et al. 4111* (MO). Pedra de Itanua, *Sucre et al. 5024* (MO). Serra do Mendanha, *Sucre et al. 6555* (MO). MARANHÃO: 35 km S of Loreto, *Eiten & Eiten 4320* (US). São Luiz, *Fróes 11871* (F, NY, US). Vila Rondon, *Pinheiro 33* (MO).

MATO GROSSO: Vic. of Dourados, *Chase 10969* (F, MO, NY, US). Santa Amia da Chapoda, *Malme 3357* (US). MINAS GERAIS: Juiz de Fóra, *Chase 8610* (F, US). Lavras, *Chase 8788.5* (US). 110 km NE of Bello Horizonte, *Chase 9103* (F, GH, MO, NY). Serra do Curral, *Chase 9304* (US). Viçosa, *Chase s.n.* (US). Ca. 15 km W of Pará de Minas, *Davidse & Ramamoorthy 10816* (ISC, MO). Ca. 27 km SE of Coroaci, *Davidse et al. 11477* (ISC, MO). Ca. 8 km N of Teófilo Otoni, *Davidse et al. 11500* (MO). Parque Estadual do Rio Doce, *Heringer & Eiten 15025* (MO), *15106* (MO), *15220* (MO). Visçosa, *Irwin 2741* (F, NY, UC). Serra do Espinhaço, *Irwin et al. 23138* (MO). 15 km N of São Jão da Chapada, *Irwin et al. 28160* (MO, NY, US). Visçosa, *Kuhlmann 1951* (ISC, MO), *1952* (US). Bello Horizonte, *Kuhlmann s.n.* (MO, US). Viçosa, *Mexia 5328* (F, GH, MO, NY, UC, US). Itabira, *Sampaio 7041* (US). PARÁ: Belém, *Archer 8254* (US). Urucuribaba, *Archer 8403* (US). Vic. of Pará, *Baker s.n.* (US). Belém, *Black & Murça Pires 122* (RB). Belterra, *Black 47-1052* (US). Rio Tapajós, *Dahlgren & Sella 198* (F, US); *Ducke s.n.* (RB-79247). Bragança River, *Goeldi 38* (F, MO, NY, US), *70* (NY, US). Majaró Island, *Goeldi 227* (F, US). Vic. of Pará, *Killip & Smith 30379* (NY, US). Vic. of Santarém, *Kuhlmann 2002* (MO, US). Peixe River, *Pires 3389* (COL, UC). Serra do Cachimbo, *Prance et al. 25017* (MO). Vic. of Paragominas, *Prance & Silva 58699* (MO). Altamira, *Silva et al. AS185* (MO). São Goetamo, *Silva 660* (US). Santarém, *Silva & Souza 2247* (MO, NY). Belém, *Soderstrom 1198* (US). Boa Vista, *Swallen 3175* (RB, US). Aramanshy, *Swallen 3215* (RB, US). Mosqueira, *Swallen 4871* (US), *4879½* (US). Santa Isabel, *Swallen 5051* (ISC, RB, US). Near Santarém, *Zery 531* (F). PARANÁ: Yacarchy, *Dusén 6605* (GH), *7898* (MO, NY). Alexandria, *Dusén 11487* (MO, NY, US). Yacarchy, *Dusén 14050* (GH, MO, US). Pinheirinho, *Hatschbach 14091* (F). Tararchy, *Jönsson 138A* (F, UC, US). Rolandia, *Swallen 8756* (US), *8757* (US). Rio do Vargen, *Swallen 9005* (US). PERNAMBUCO: Garanhuns, *Chase 7833* (F, GH, MO, US). Saltinho, *Falcão et al. 912* (MO, RB). Olinda, *Leal & Silva 14* (MO). Tapera, *Pickel 49* (F), *106* (US), *1359* (US), *s.n.* (F, GH). Recife, *Tenório s.n.* (MO). RIO DE JANEIRO: Ilha Queimada, *Amaral & Domingues 3935* (US). Serra da Estrella, *Brade 20104* (US). Serra Carioca, *Carauta 833* (RB). Bay of Rio, *Chase 8385* (US). Corcovado, *Chase 9744* (F, GH, MO, NY, US). Vic. of Rio de Janeiro, *Chase 9796* (F, US). Furnas do Agassiz, *Chase 12131* (US). Env. de Rio de Janeiro, *Commerson s.n.* in 1767 (P). Parati, *Eiten & Eiten 6279* (MO). Rio de Janeiro, *Gaudichaud 303* (P). Inoõ, *Gomes et al. 1217* (RB, US). Restinga da Tijuca, *Machado 78* (RB), *s.n.* (MO, RB). Lagoinha da Gavea, *Machado s.n.* (RB). Corcovado, *Rose & Russell 20156* (NY, US), *20312* (NY, US). Rio de Janeiro, *Saint-Hilaire 126* (P). Vic. of Meio da Serra, *Smith & Brade 2284* (F, GH, NY, UC, US). Velha–Petrópolis, *Soderstrom & Sucre 1872* (MO). 2 km SW of Baira, *Soderstrom & Sucre 1914* (MO). Between Cachoeiro de Macacu and Nova Friburgo, *Soderstrom & Sucre 1976* (MO). Ilha Furtada, *Sucre & Bragga 2588* (MO), *2628* (MO). Pedro de Rio, *Sucre & Bragga 2644* (MO). Petrópolis, *Sucre & Bragga 4239* (MO). Rio Vermelho, *Sucre & Silva 9168* (MO). Env. de Rio de Janeiro, *Weddell 255* (P). RONDÔNDIA: Abunã to Rio Branco, *Prance et al. 5954* (MO). 1 km N of Riberão, *Prance et al. 6451* (MO). Vic. of São Lorenço mines, *Prance et al. 8926* (MO). São Luiz, *Rosa 813* (MO). RORAIMA: Serra Tepequem, *Prance et al. 4311* (MO, US). SANTA CATARINA: Itajaí, *Klein 1194* (US), *1305* (US), *1320* (US). Moro de Inglezes, *Klein et al. 6689* (US). Ilha Santa Catarina, *Reitz & Klein 727* (US). Morro da Fazenda, *Reitz & Klein 1711* (NY, UC, US). Itají, *Reitz & Klein 1958* (US), *2874* (NY, UC, US), *2951* (US). SÃO PAULO: E of Pôrto Alvorado, *Eiten et al. 5995* (MO). Nova Europa, *Hoehne 13613* (GH, US). Mogy to Mirim, *Hoehne 20404* (NY, US). Araraquara, *Loefgren 9799* (US). Pindorama, *Mendes 4557* (US). Loreto, *Sampaio 4486* (US). Campinas, *Viegas 3839* (US).

COLOMBIA. AMAZONAS: Río Loretoyacu, *Black & Schultes 46-185* (US); *Schultes & Black 8313* (GH, US). Río Orteguaza, *Woronow & Juzepczuk 6379* (US). CUNDINAMARCA: 28 km NE of Gachela, *Grant 10549* (US). PUTUMAYO: Río San Miguel en la Bermeja, *Cuatrecasas 11025* (COL, F, US).

DOMINICAN REPUBLIC. DISTRITO NACIONAL: Vic. of Ciudad Trujillo, *Allard 16374* (US). LA VEGA: Vic. of Piedra Blanca, *Allard 13333* (A, US), *17779* (US), *17785* (US). La Cumbre, *Augusto 502* (NY). MARIA TRINIDAD SÁNCHEZ: Río San Juan, *Miller 1184* (US). SAMANÁ: Vic. of Sánchez, *Abbott 121* (GH, IJ, US).

ECUADOR. NAPO: El Napo, *Benoist 4743* (P). Santa Cecilia, *Dwyer & Simmons 9753* (MO). Near Tena, *Mexia 7218* (F, UC, US). Limoncocha, *Mowbray 69946* (NY). PASTAZA: 20 km along Río Pastaza, *Holm-Nielsen & Jeppesen 578* (AAU). PICHINCHA: NE of Tandayapa, *Solís 17159* (US). TUNGURAHUA: Between Baños and Cashurco, *Hitchcock 21863* (US).

FRENCH GUIANA. Vic. of Cayenne, *Broadway 225* (GH, NY, US), *389* (GH, NY, US), *415*

(GH, NY, US), 533 (US), *654* (GH, NY, US), *685* (GH, US), *712* (GH, NY, US). Saül, *Descoings & Luu 20539* (CAY); *de Granville B-4419* (CAY). Trois Sauts, *Grenand 524* (CAY, MO); *Lescure 384* (CAY); *Haxaire 962* (CAY). Cayenne, *Hoock s.n.* (NY), *89* (CAY). Rivière Comté, *Oldeman B-2063* (CAY). Ile de Cayenne, *Oldeman B-3485* (CAY). Saül, *Oldeman B-3926* (CAY), *B-4217* (CAY). Haut Maroni, *Sastre et al. 3864* (CAY, MO).

GUAYANA. NORTHWEST: Waini River, *La Cruz 1132* (MO), *3663* (F, GH, MO, NY, UC, US). Assakatta, *La Cruz 4291* (F, GH, MO, NY, UC, US), *4313* (F, GH, MO, NY, UC, US). POMEROON: Maruka River, *La Cruz 2544* (F, GH, MO, NY, UC, US). Pomeroon River, *La Cruz 2931* (F, GH, NY, US). DISTRICT UNKNOWN: Aruka River, *Fanshawe 5127* (A, NY). Potaro River, *Gleason 70* (GH, NY, US); *Hitchcock 17345* (US), *17553* (F, GH, MO, NY, UC, US), *17567* (US). Upper Demarara River, *Jenman 4089* (US). Isherton, *Smith 2417* (F, GH, NY, US).

PERU. AMAZONAS: E of Huampami, *Berlin 1514* (MO). Quebrada Huampami, *Kayap 903* (MO). Quebrada Wampushik, *Kayap 952* (MO). 1 km SE of Yambrasbamba, *Wurdack 1048* (F, NY, US). Shipsbamba to Pomacocha, *Wurdack 1096* (F, NY, US). Valley of the Río Marañon, *Wurdack 1807* (F, NY, RB, UC, US). AYACUCHO: Aina, *Killip & Smith 22724* (NY, US). Near Kimpitiriki, *Killip & Smith 22937* (F, NY, US). Estrella, *Killip & Smith 23080* (NY, US). CUZCO: Prov. Pancartambe, *Marin 1526* (F); *Vargas 14695* (US). HUÁNUCO: Vic. of Tingo Maria, *Belshaw 3086* (F, GH, MO, NY, UC); *Ferreyra 920* (US), *13141* (US). Villa Isabel to Cuchares, *Woytkowski 1258* (GH, MO). JUNÍN: Vic. of Colonia Perene, *Hitchcock 22116* (US), *22119* (US). 9 km SW of San Ramón, *Iltis et al. 313* (ISC, WIS). La Merced, *Killip & Smith 23451* (F, NY, US). San Ramón, *Killip & Smith 24896* (NY, US). Vic. of Colonia Perene, *Killip & Smith 24987* (NY, US), *25255* (NY, US). Puerto Yessup, *Killip & Smith 26327* (F, NY, RB, US). Cahuapanas, *Killip & Smith 26726* (F, GH, NY, US). San Francisco de Satipo, *Solomon 3240* (MO). LORETO: Santa Maria below Yurimaguas, *Anderson 770* (UC, US). Iquitos, *Asplund 13994* (US), *14378* (NY, US). Piscigranja Quistococha, *Ayala 693* (MO). Río Paranapura, *Croat 17874* (MO). Quebrada Tahuayo, *Croat 19761* (MO). Vic. of Aguaytia, *Croat 21008* (MO). Iquitos, *Killip & Smith 27088* (F, NY, US), *27125* (F, NY, RB, US). Vic. of Yurimaguas, *Killip & Smith 27561* (F, NY, US), *28266* (NY, US), *29085* (F, NY, US). Iquitos, *Klug 1398* (F, NY, US). Intute, *McDaniel 10801* (MO). Near Iquitos, *McDaniel 11722* (MO). Río Ampiyacu, *Revilla 921* (MO). Pucallapa, *Soukup 3055* (F). Lower Río Nanay, *Williams 399* (F, US). Pinto–Cocha, *Williams 781* (F, US), *789* (F, US). Caballo to Cocha, *Williams 2035* (MO). Alto Rio Itaya, *Williams 3241* (F, US), *3262* (F). Iquitos, *Williams 3717* (F, US). Lower Río Huallaga, *Williams 4780* (F, US). SAN MARTIN: Tingo Maria, *Allard 22244* (US). Near Tarapoto, *Ferreyra 7775* (US). Above San José de Sisa, *Ferreyra 7916* (US). Río Huallaga Canyon, *Macbride 4250* (F, GH). Tarapoto, *McDaniel 13732* (MO). Puerto Pizana, *Schunke 6993* (MO). Sapososa, *Woytkowski 8349* (MO).

PUERTO RICO. Vic. of Mayagüez, *Britton & Marble 678* (F, NY, US). Near Maricao, *Britton et al. 4490* (F, GH, NY, US). Vic. of Arecibo, *Chase 6454* (US). Vic. of Cayey, *Chase 6734* (US), *6747* (US). Guavate, *Liogier 10418* (GH, IJ, NY, US). Maricao, *Sintensis 215* (GOET, NY, US). Near Larerx, *Sintensis 5918* (US). Luquillo Mts., *Wilson 350* (NY, US).

SURINAM. Sandrij Island, *Archer 2759* (US). Oelemani, *Boer 1158* (NY, UC). Vic. Moego, Cottica River, *Cowan 39007* (NY, US). Brokobaka, *Donselaar 3838* (A, F). Kalalebo, *Florschütz & Maas 2495* (US). Lucie Rivier, *Irwin et al. 55790A* (MO). Wilhelmine Gebergte, *Irwin et al. 57618* (MO, NY, UC, US). Coppername to Coronie, *Lanjouw & Lindeman 1384* (NY). Nassau, *Lanjouw & Lindeman 2146* (NY). 3 km N of Paramaribo, *Maguire & Stahel 22746* (A, F, NY). Pakka Pakka, Saramacca River, *Maguire 23965* (F, GH, MO, NY, RB, US). Tafelberg, *Maguire 24315* (NY). Montagne Ischoli–Epoyan, *Sastre 1460* (CAY). Wilhelmine Gebergte, *Stahel 621* (MO).

TOBAGO. Old Castara Rd., *Andrew 610A* (NY). Belmont Woods, *Broadway 3551* (F, ISC, MO, US). *Broadway 4038* (F, NY, US). Roxborough-Parlatuvier Rd., *Cowan 1410* (NY, US), *1486* (NY, US). Center of island, *Hitchcock 10261* (US), *10262* (US), *10269* (US), *10275* (US).

TRINIDAD. Caparo Woods, *Broadway 4923* (US). Tamana Forest, *Broadway 4952* (RB, US), *4959* (RB, US). Blanchisseuse Rd., *Broadway 5504* (A, MO). Aripo Rd., *Broadway 5892* (MO, US). Arouca, *Broadway 6811* (F, MO, US). Monga, *Broadway 7915* (US). Heights of Aripo, *Broadway 9929* (GH, NY, US). Morne Blue, *Britton et al. 2266* (GH, NY, US). Northern Range, *Davidse 2461* (MO). Between La Vache and

Maracas Bay, *Davidse 2566* (ISC, MO). Ca. 2 mi NE of Point Fortin, *Davidse 2579* (MO). Maraval, *Hart 5427* (M). Port of Spain, *Hitchcock 9962* (US). St. Joseph, *Hitchcock 10020* (US). Tabaquite, *Hitchcock 10120* (US). Cedros, *Hitchcock 10151* (US). Valencia-Matura Rd., *Soderstrom 1036* (US).

VENEZUELA. BOLÍVAR: Km 88, carretera El Dorado, *Aristeguieta 3712* (VEN). Cerro Uroi, *Maguire et al. 53806* (VEN). La Gran Sabana, *Tamayo 2786* (US, VEN).

VIRGIN ISLANDS. ST. CROIX: Bodkin Hill, *Fosberg & Ogden 55312* (MO). ST. THOMAS: *Britton & Marble 1230* (NY, US). TORTOLA: Sage Mtn., *Shafer 1147* (NY, US).

WINDWARD ISLANDS. GUADELOUPE: *Bertero s.n.* (P).

6. **Lasiacis linearis** Swallen, Phytologia 4: 427. 1953. TYPE: Guatemala, Zacapa, Sierra de las Minas, below Finca Alejandria, pine covered canyon bordering Río Lima, 2000 m, 14 Oct. 1939, *Steyermark 30046* (F, holotype).

Perennial; main culms creeping, decumbent, rooting at the nodes, only the ultimate portions erect, these commonly 40–100 cm tall, occasionally higher when supported in brush, the culms freely branching and forming large tangled colonies; internodes slender, 2–5 mm thick, solid, often purplish, usually glabrous, occasionally with a small line of puberulence, or the upper part puberulent; nodes glabrous; sheaths puberulent or pubescent with hairs to 0.7 mm long, the overlapping margin ciliate, with hairs to 0.5 mm long, rarely glabrous, sheaths mostly shorter than the internodes; ligule conspicuous, (1.4–)1.8–4.0(–4.8) mm long, tan to dark brown, the apex irregularly erose to lacerate, ciliate with hairs 1.5–3.0 mm long, puberulent to short pubescent on the back; collar densely puberulent throughout, rarely only on the margin; blades 13–22 cm long, 0.8–1.5(–1.18) cm wide, the base slightly asymmetrical, the apex acuminate to attenuate, the upper surface usually glabrous and often scabrid, occasionally short pubescent especially toward the base, the lower surface usually glabrous, occasionally sparsely puberulent especially along the midrib, the margins scabrid; panicles 19–30 cm long, the longest branch 10–23 cm long, the branches scabrid, widely spreading, naked at least for the lower half, bearing long-pedicelled spikelets toward the ends of the branches, the pulvini glabrous, the lower ones often puberulent with a few short hairs; spikelets narrow, obovate, 3.9–4.5 mm long, 2.2 mm wide, often purplish when immature; first glume 2.0–2.5 mm long, 7–9-nerved; second glume 8–11-nerved; sterile floret without a flower, the lemma 9–11-nerved, the palea usually ⅓ to ½ or rarely ⅔ as long as the fertile floret, occasionally absent; fertile floret 3.9–4.1 mm long, 2.0–2.4 mm wide, the anthers white, the stigmas purple; caryopsis 2.2–2.4 mm long, 1.6–1.8 mm wide; chromosome number $n = 18$.

Ecology: *Lasiacis linearis* typically inhabits cloud forests although it may often extend down into the oak-pine and pine communities which commonly occur below cloud forests in northern Central America. It may often be found in fairly undisturbed sites, especially in the pine forests. In the cloud forests, it is usually more common in habitats where some disturbance has taken place, such as along trails, in partially logged areas, in open areas created by downed trees, and along forest edges. The species has been collected in the mountains from 1,400 to 2,400 m. Spikelet-bearing plants have been collected in June, July, and October through March.

Distribution: *Lasiacis linearis* is an infrequent species extending from Chiapas, Mexico, to eastern Panama. I have seen no collections from Belize, El Salvador, and Nicaragua.

Lasiacis linearis is characterized by its procumbent growth habit, solid culms, long narrow blades, prominent ligules, and the diffuse panicles with few, solitary, long-pedicelled spikelets. Occasional specimens do not have completely solid culms. I have seen four collections in which this is true, *Davidse & Pohl 2121*, *Morton 6954*, and *Standley 23126* from Honduras and *Williams et al. 26097* from Guatemala. Some culms in these collections may be completely solid whereas in others the pith may be partly missing. In all cases, however, one can see some definite pith remains or partial cores. The brown appearance of the pith in some specimens suggests that some of the destruction may be due to fungal growth, and in others, insect destruction seems probable.

Lasiacis linearis is most closely related to *L. oaxacensis* and is probably a montane-forest derivative of the latter. The two are much alike in growth form and gross morphology, but *L. oaxacensis* is generally more robust in all respects. In Central America, where the two species are sympatric, they can best be distinguished by the glabrous sheaths and by the clustering of the spikelets in pairs or small groups toward the tips of the panicle branches in *L. oaxacensis* and in the lack of staminate flowers in the sterile floret of *L. linearis*.

Lasiacis linearis has often been identified as *L. lucida*. The type of *L. lucida*, however, belongs with *L. standleyi* which has hollow culms and a more densely flowered panicle than *L. linearis*.

Lasiacis linearis was long known only from the type collection in Guatemala (Swallen, 1955a). Recent collections have extended the range of this species throughout most of Central America, with the exceptions of Belize, El Salvador, and Nicaragua. It is almost certain to be found in Nicaragua, a country which for the most part is the most poorly collected area in Central America. Whether it occurs in Belize and El Salvador is more problematical. In El Salvador it should be looked for in the northern part of the county.

Common name: Panama: Chiriqui, bambito, *Tyson 5666*.

COSTA RICA. ALAJUELA: La Brisa de Zarcero, *Smith H978* (F). SAN JOSÉ: 2 km from San Gabriel, *Pohl & Davidse 11049* (ISC).

GUATEMALA. EL PROGRESO: Sierra de las Minas, *Steyermark 43405* (F, US). GUATEMALA: Vic. of San Andrecillo, *Molina & Molina 27555* (MO). QUINCHÉ: 2.5 mi N of Nebaj, *Proctor 25497* (IJ). S of Chichicastenango, *Standley 62422* (F). SAN MARCOS: Near Aldea Fraternidad, *Williams et al. 26097* (F, GH, NY, US). SOLOLÁ: Volcán Atitlán, *Steyermark 47347* (F, US). ZACAPA: Sierra de las Minas, *Steyermark 30046* (F), *42496* (F, US).

HONDURAS. EL PARAÍSO: Güinope, *Rodríguez 1760* (F). MORAZÁN: Cerro Uyuca, *Davidse & Pohl 2100* (ISC, MO), *2106* (ISC, MO). Cerro La Tigre, *Davidse & Pohl 2121* (ISC, MO). Cerro Uyuca, *Glassman 1625* (F, NY). Mt. San Juancito, *Glassman 1972* (NY, UC). Cerro La Tigre, *Hawkes et al. 2131* (F, US). Cerro Uyuca, *Molina 205* (F, GH, US); *Morton 6954* (F, NY, US); *Pohl 12490* (ISC); *Standley & Williams 690* (F); *Standley 4798* (F), *23126* (F, GH, NY, UC, US), *28282* (F, GH); *Swallen 10900* (US), *11057* (US). Mt. San Juancito, *Swallen 11138* (US). Cerro Uyuca, *Williams & Molina 12112* (US).

MEXICO. CHIAPAS: Sierra Madre, *Tateoka 1031* (US).

PANAMA. CHIRIQUÍ: Cerro Azul, *Croat 26858* (MO). Volcán de Chiriquí, *Davidse & D'Arcy 10162* (MO); *Hitchcock 8201* (US). Ca. 2 mi W of Cerro Punta, *McDaniel 10048* (MO). Monte Lirio, *Seibert 278* (GH, MO, NY, US). 1 mi SW of Cerro Punta, *Tyson 5666* (MO). Cerro Punta, *Tyson 5802* (MO, SCZ). Near El Volcán, *White 218* (MO).

7. **Lasiacis nigra** Davidse, Phytologia 29: 152. 1974. TYPE: Costa Rica, Alajuela, 3 km N of Palmares along the Carretera Interamericana, 800 m, edge of coffee plantation, culms 8 m tall, hanging from trees, 22 Oct. 1968, *Pohl & Davidse 11272* (ISC, holotype; CR, EAP, K, MO, US, isotypes).

Panicum divaricatum L. var. *molle* Schlecht. & Cham., Linnea 6: 33. 1831. TYPE: not indicated.

Perennial; culms, casepitose, erect at the base, arching above and clambering into vegetation, 1–8 m long; internodes to 10 mm thick, lignified, glabrous, with a line of puberulence, papillose-puberulent, or densely papillose-pubescent, hollow; nodes glabrous; sheaths pilose or varying to completely glabrous, the margin cilate with hairs to 3.0 mm long, the auricular hairs to 4.0 mm long; collar pilose, puberulent, or glabrous; ligule 0.5–1.3(–2.0) mm long, usually whitish and glabrous or occasionally darker and pubescent on the back, the apex glabrous or ciliate with hairs to 1.5 mm long; blades linear to lanceolate, 5–11(–15) cm long, (0.3–)0.6–1.8(–2.6) cm wide, commonly pilose, also puberulent, pubescent, or completely glabrous, the base asymmetrical, slightly lobed and clasping the culm, the margin scabrid, the apex acuminate; panicles (2–)5–12(–19) cm long, the longest branch 1–8(–11) cm long, bearing few, long-pedicelled spikelets, the branches ascending to diverging, branches pilose to glabrous, the pulvini pilose to glabrous, the pedicels widely spreading at maturity; spikelets large, obovate, (3.6–)4.0–5.0(–5.5) mm long, often purple when immature; first glume (1.6–)2.0–2.7(–3.2) mm long, 5–13-nerved; second glume 7–13-nerved; sterile floret with or without a staminate flower, the anthers rudimentary or 2.3–2.7 mm long, the lemma 9–11-nerved, the palea ½ to subequal the length of the fertile floret; fertile floret 3.8–4.6 mm long, 2.5–2.9 mm wide, brown, the anthers 2.1–2.8 mm long, white, the stigmas white; caryopsis 2.4–2.7 mm long, 1.9–2.4 mm wide, light brown; chromosome number $n = 18$.

Ecology: *Lasiacis nigra* is a montane species primarily found along forest edges, in roadside thickets, and among similar secondary woody vegetation. It is found as a component of deciduous forests, pine-oak forest, and montane broadleaf forests. Most elevation records are between 900 to 2,300 m. A few collections from South America have been reported from subalpine páramo vegetation at 2,600 m in the Andes, the highest elevation record for any *Lasiacis* species. Spikelet-bearing plants have been collected throughout the year but most commonly from June to January.

Distribution: *Lasiacis nigra* extends from southern Nuevo León and Tamaulipas in Mexico south throughout Central America. In northwestern South America, it occurs in Colombia, Venezuela, Ecuador, and Peru.

Hitchcock (1920) interpreted *L. sorghoidea* very broadly, including under it *L. sorghoidea* var. *sorghoidea* and *L. nigra* of my treatment. At the same time, he raised the possibility that more than one taxon should be recognized.

I believe that two species are included under *L. sorghoidea* sensu Hitchcock, namely *L. nigra* and *L. sorghoidea*. *Lasiacis nigra* is more delicate and scandent that *L. sorghoidea*; it has smaller leaves and inflorences but usually larger spikelets; and its inflorescence bears relatively few, large, long-pedicelled spikelets

giving it an open appearance. *Lasiacis sorghoidea*, on the other hand, typically has large, moderately dense inflorescences with many small spikelets on short pedicels. The most common type of leaf pubescence pattern in *L. sorghoidea* is one in which the sheaths are papillose-hispid, the collar is densely hispid, the lower blade surface is velutinous, and the upper blade surface is puberulent or hispidulous. This pattern is rarely encountered in *L. nigra* in which pubescence varies from nearly completely glabrous to densely pilose.

Even with the exclusion of *L. sorghoidea*, *L. nigra* still remains morphologically variable. I have not chosen to give formal taxonomic recognition to any variants, but further study may show the desirability of doing so. Some of the major features of variation are discussed below.

Included in *L. nigra* are plants with relatively long, narrow leaves, usually glabrous or nearly so, but at times pubescent. These generally bear spikelets approaching the largest size in *L. nigra*. They are concentrated in South America and Mexico. Many of the South American specimens have been identified as *L. leptostachya* (=*L. divaricata* var. *leptostachya*) in recent years. However, the long-pedicelled, widely spreading spikelets distinguish these plants readily from that strictly Central American and Mexican variety of *L. divaricata*. Another form, especially common in Central America but known from throughout the range, is one with relatively broader and shorter pilose leaves and relatively large spikelets. A third common form is one which may have pubescent or nearly glabrous leaves, often with just a few large hairs along the midrib. The spikelets may be small or large and leaf size tends to be intermediate between that of the previous two forms. The small-spikelet specimens of this third form are some of the most puzzling in the genus. They have often been identified as *L. divaricata* var. *divaricata* but are closer to *L. sorghoidea* and *L. divaricata* var. *austroamericana*. *Lasiacais divaricata* var. *divaricata* can most easily be distinguished on the basis of its divergent panicle branches and larger spikelets. *Lasiacis sorghoidea* can best be distinguished by the usually less densely arranged spikelets and larger blades. From *L. divaricata* var. *austroamericana* these specimens differ in their pubescence. Admittedly the distinctions become rather arbitrary. But the number of specimens is relatively small, and since they are mostly from higher elevations, it seems most appropriate to include them with *L. nigra*. Representative specimens are listed separately after the more typical collections of *L. nigra*.

Lasiacis nigra probably represents the same taxon as *L. divaricatum* var. *molle*. Both the two-word description (villoso-pubescens) and the geographical location where these plants were collected (Veracruz to Jalapa) indicate that var. *molle* may be the same as *L. nigra*. However, I have not seen the type, which is presumably located at Halle (HAL) (Stafleu, 1967).

BELIZE. CAYO: *Lundell 6434* (F, GH, NY, US). San Augustin, *Lundell 6752* (F, GH, NY, US).

COLOMBIA. ANTIOQUIA: Bello, *Archer 174* (US). Vic. of Medellín, *Archer 374* (US). Granja de las Mercedes en Venecia, *Barkley & Gutiérrez 1651* (US); *Barkley et al. 17C448* (US). W of Frontino, *Core 477* (US). Laguna de Guarne, *Daniel 2770* (US). Caldas, *Gärtner 38* (US). Vic. of Medellín, *Jaimes 9* (US); *Molina & Barkley 19An076* (F, US), *19An078* (US), *19An079* (F, US). Caldas, *Rodríguez 19* (US). Vic. of Medellín, *Toro 833* (NY); *Varela 17* (US). CALDAS: Salento, *Killip & Hazen 8770* (GH, NY, US). CAUCA: Between Rosale and

Bolívar, *Core 124* (US). Popoyán, *Cuatrecasas & Arbeláez 6080* (F, US). Tacueyó, *Cuatrecasas 19377* (F, GH, US). El Paraíso, *Dryander 2056* (UC, US). 5 km E of Timbío, *Grant & Drew 10667* (US). Río Sucio, *Pennell & Killip 7223* (NY, US), *7227* (US). Cuesta de Tocatá, *Pittier 685* (US). Miraflores, *Pittier 886* (US). El Tambo, *Sneidern 164* (GH, US). CUNDINAMARCA: La Hondonada, *Cuatrecasas 221* (F, US). Sasaima, *García-Barriga 12598* (US). Vic. of Bogotá, *Grubb et al. 843* (US). Fusagasuga, *Juzepczuk 5280* (US). Cagueza, *Karsten s.n.* (GOET, US). Fusagasuga, *Koie 5237* (US). HUILA: 23 km ENE of Colombia, *Fosberg 19635* (US). 15 km ENE of Colombia, *Fosberg 19649* (US). Between Acevedo and Suaza, *Little 8556* (US). E of Neiva, *Rusby & Pennell 861* (GH, MO, NY, US), *1001* (NY, US). MAGDALENA: SE of Donachuí, *Cuatrecasas & Romero-Castañeda 24325* (US). E of Manuure, *Cuatrecasas & Romero-Castañeda 25306* (US). Sierra de Santa Marta, *Kirkbride 2302* (MO), *2446* (MO). Alrededores de San Andrés, *Romero-Castañeda 6974* (MO). NARIÑO: Pasto, *Alston 8292* (US). Vic. of Samaniego, *Fernández & Mora 1188* (NY). 22 km E of Pasto, *Fosberg 20532* (US). Between Cartago and La Unión, *Mora 2407* (US). SANTANDER: Above Suratá, *Killip & Smith 16554* (US). Vic. of California, *Killip & Smith 17013* (GH, NY, US), *17690* (GH, US). TOLIMA: Libano, *Pennell 3415* (MO). VALLE: El Cairo, *Cuatrecasas 13884* (F). Between San Antonio and Mares, *Cuatrecasas 15202* (F, UC, US). Naranjal, *Cuatrecasas 15358* (F, US). La Tulia, *Cuatrecasas 18532* (US), *18572* (F). Between Brisas and Alban, *Cuatrecasas 22174* (F, US). Las Nieves, *Dryander 1895* (US). Dugua, *Killip 5444* (GH, NY, US). La Cumbre, *Killip 5680* (GH, NY, US); *Killip & Hazen 11117* (GH, NY, US). El Silencio, *Killip & García 33793* (US). La Cumbre, *Pennell 5025* (GH, NY, US). Cartago, *Rojas 4* (US).

COSTA RICA. ALAJUELA: La Palma de San Ramón, *Brenes 5147* (F, US), *5161* (US), *5191* (F, NY). Santiago near San Ramón, *Brenes 14375* (GH). La Palma de Ramón, *Brenes 15059* (F, NY). Vic. of San Ramón, *Brenes 17025* (F). Carillos de Poás, *Brenes 19413* (F, NY). Vic. of San Ramón, *Brenes 20314* (F, NY), *20507* (F). San Miguel de San Ramón, *Brenes 21952* (F). Cocao de Alajuela, *Brenes s.n.* (NY). La Palma, *Maxon & Harvey 7998* (GH, NY, US), *8025* (US), *8050* (US). 6.5 km W of Vara Blanca, *Pohl & Calderón 10280* (ISC). Volcán Poás, *Pohl & Davidse 11174* (ISC). 1 km S of Ciudad Quesada, *Pohl & Davidse 11250* (ISC). 3 km N of Palmares, *Pohn & Davidse 11272* (ISC). 10 km N of San Ramón, *Pohl & Davidse 11275* (ISC). La Palma de San Ramón, *Pohl & Davidse 11371* (ISC). Guadeloupe de Zarcero, *Smith A371* (F, MO). Region of Zarcero, *Smith A430* (MO). San Luis de Zarcero, *Smith H1015* (F, MO, NY). Vic. of Fraijanes, *Standley & Torres 4705* (US). La Palma, *Stork C423* (UC). Santa Clara, *Stork 2577* (US). CARTAGO: Vic. of Cartago, *Brenes 10423* (US); *Cooper 98* (US). Cervantes, *Carpenter 662* (US). Vic. of Tablazo, *Durkee 75-60* (MO). 3 km E of Cachí, *Lent 1736* (F, NY). Vic. of Santiago, *Maxon 128* (NY, US). Moravia de Chirripó, *Pohl & Davidse 10870* (ISC). 10 km SW of Tejar, *Pohl & Davidse 11134* (ISC). 9 mi S of Purasil, *Pohl & Davidse 11198* (ISC). 3 km W of Grano de Oro, *Pohl & Davidse 11477* (ISC). Platanillo, *Smith 3019* (ISC). Vic. of Cartago, *Standley 33365* (NY, US). El Muñeco, *Standley 33581* (US). La Estrella, *Standley 39215* (GH, US). Vic. of Orosí, *Standley 39648* (US). Río Ventado, *Standley & Valerio 49448* (US). 3 km from Tejar, *Taylor & Taylor 11866* (MO). Alto de Ochomogo, *Williams & Molina 13821* (F, GH, MO). HEREDIA: Río Virilla, *Allen 591* (F, GH, MO). 5 km NE of Vara Blanca, *Davidse 892* (NY). Río Vueltas, *Gómez 2290* (F). Vara Blanca, *Skutch 3148*. LIMÓN: 19 mi below IICA, *Pohl & Calderón 10310* (ISC). PUNTARENAS: E of Monteverde, *Burger & Baker 9578* (MO). Between Buenos Aires and Cerro Pittier, *Hatheway 1689* (US). Cañas Gordas, *Pohl & Davidse 11166* (ISC). Hatillo, *Rojas 46* (F). San Vito de Java, *Smith 2938* (ISC). SAN JOSÉ: Río Tirribí, *Alfara 33989* (GH, US). San Fernando de Guadeloupe, *Canossa s.n.* (F). Vic. of San José, *Hitchcock 8451* (US); *Pittier 81A* (US). 10 km NE of San Isidro del General, *Pohl & Calderón 10048* (ISC). 4 mi S of División, *Pohl & Davidse 10070* (ISC). Between Aserrí and Tarbaca, *Pohl & Calderón 10388* (ISC). 7 km S of Aserrí, *Pohl & Davidse 11041* (ISC). 2 km NNE of San Gabriel, *Pohl & Davidse 11050* (ISC). 1 km E of Frailes, *Pohl & Davidse 11071* (ISC). Below La Hondura, *Pohl & Davidse 11214* (ISC). S of San Antonio, *Pohl & Davidse 11351* (ISC). 0.5 km SE of Barbacoas, *Pohl & Davidse 11403* (ISC). 7 km S of Aserrí, *Riggins 606* (ISC). La Hondura, *Smith 2843* (ISC). Vic. of San José, *Standley 38998* (US). Between San Pedro Montes de Oca and Curridabat, *Standley 41296* (US). Between Aserrí and Tarbaca, *Standley 41350* (GH, US). Vic. of Santa Maria de Dota, *Standley 41665* (US); *Standley & Valerio 43476* (US). Vic. of San José, *Standley 47324* (GH, US), *47328* (GH, US). Uruca, *Tonduz 7207* (F, GH, US). Between San José and Zapote, *Tonduz 7234* (F, GH, US).

ECUADOR. AZUAY: Río Noray, *Steyermark 52868* (F, US). IMBABURA: El Achiotal,

Solís 12337 (F). NAPO: Between Puyo and Canelos, *Mexia 6850* (UC, US). Puyo, *Skutch 4397* (A, F, MO, NY, US). ORO: Between La Chorita and Portovelo, *Hitchcock 21180* (US), *21184* (US). PICHINCHA: Chiriboga, *Asplund 8669* (US). Santo Domingo de los Colorados, *Fagerlind & Wibom 1961* (MO). Tandayapa, *Solís 17008* (US). Santa Domingo de los Colorados, *Solís 10895* (F). SANTIAGO ZAMORA: 18 km NE of Loja, *Fosberg 23149* (US). TUNGURAGUA: Between Baños and Cashurco, *Hitchcock 21856* (US). El Topó, *Solís 10281* (F).

EL SALVADOR. AHUACHAPÁN: Near Ataco, *Standley & Padilla 2720* (F). Vic. of Ahuachapán, *Standley & Padilla 2759* (F), *2985* (F). Vic. of Apaneca, *Standley & Padilla 2992* (F). LA LIBERTAD: Volcán San Salvador, *Davidse & Pohl 2025* (ISC, MO); *Hitchcock 8925* (US), *8951* (US), *8952* (US); *Pohl & Davidse 11831* (ISC, MO); *Pohl & Gabel 13661* (MO); *Williams & Molina 15100* (US), *15126* (US). MORAZÁN: Montes de Cacaquatique, *Tucker 693* (F, ISC, NY, UC, US), *733* (F, ISC, UC, US). SAN VICENTE: Volcán San Vicente, *Standley 21508* (GH, US). SANTA ANA: 7 mi NE of Metapán, *Croat 42290* (MO). E side of Lago de Coatepeque, *Davidse & Pohl 2035* (ISC, MO). Cerro Verde, *Pohl & Gabel 13594* (MO). Massif Monte Cristo, *Weberling 597* (M). Volcán de Santa Ana, *Weberling 1991* (M).

GUATEMALA. ALTA VERAPAZ: 10 km S of Cobán, *Harmon & Dwyer 4278* (MO). 5 km NE of Cobán, *Molina & Molina 11987* (US). Near Cobán, *Muenscher 12225* (US); *Standley 69153* (F), *69448* (F, US). 43 km NE of Cobán, *Standley 70182* (F). Between Cobán and Tres Cruces, *Standley 90259* (F). BAJA VERAPAZ: 16 mi from Salamá, *Hawkes et al. 1921* (F). CHIMALTENANGO: Chimaltenango to San Martin Jilotepeque, *Standley 57903* (F, NY, US), *80893* (F). Río Guacalate, *Standley 81040* (F). EL PROGRESO: 8 km S of El Progreso, *Iltis G-73* (WIS). Around Barranquillo, *Steyermark 46406* (F, US). ESCUINTLA: Volcán de Fuego, *Standley 64544* (F). GUATEMALA: Finca la Aurora, *Aguilar 31* (F). 7 mi E of Guatemala, *Harmon 2935* (MO). Guatemala, *Hitchcock 9057* (US), *9101* (US); *Kellerman 4735* (US). 20 km E of Guatemala, *Molina 13493* (US). Río Villalobos, *Molina 16067* (F, GH, NY). Between San Lucas and Guatemala, *Molina 21108* (F, NY). Amatitlán, *Ruano 843* (F). Guatemala, *Standley 59518* (F). Amatitlán, *Standley 61266* (F), *61411* (F). 10 km S of San Raimundo, *Standley 62898* (US), *62918* (US). HUEHUETENANGO: Nentón, *Seler 2858* (GH). Naxacranal, *Seler 3004* (F, GH, US). 13 km W of Huehuetenango, *Standley 81531* (F). Between Mimanhuitz and Yulhuitz, *Steyermark 48627* (US). 10 km W of Huehuetenango, *Williams et al. 22295* (F, US). JALAPA: Vic. of Jalapa, *Standley 76445* (F). Between Jalapa and Paraíso, *Standley 77336* (F). QUETZALTENANGO: Near Zunil, *Skutch 986* (A, F, ISC, US). Near Santa Maria de Jesús, *Standley 67263* (F, UC), *68268* (F, US), *84840* (F, US), *86807* (F, NY), *87004* (F, UC), *87067* (F). Between Colomba and Las Mercedes, *Standley 87968* (F, US). Near Santa Maria de Jesús, *Steyermark 33767* (F). Near Zunil, *Williams et al. 22982* (F, US), *23032* (F, NY, US). SACATEPÉQUEZ: Vic. of Santa Maria de Jesús, *Hunnewell 17090* (GH). Near Las Lajas, *Standley 58102* (F, US). Vic. of Antigua, *Standley 58590* (F, GH, US). Cuesta de las Cañas, *Standley 58962* (F, US). Vic. of Santa Maria de Jesús, *Standley 59365* (F). Above Pastores, *Standley 60762* (F). Vic. of Antigua, *Standley 61205* (F, US). Above Dueñas, *Standley 63194* (F, MO, NY). SAN MARCOS: Volcán Tajumulco, *Steyermark 37137* (F, US). SANTA ROSA: E of Cuilapa, *Standley 78219* (F). Volcán de Tecuamburro, *Standley 78566* (F). SOLOLÁ: Volcán Atitlán, *Steyermark 47982* (F, US). ZACAPA: Sierra de las Minas, *Steyermark 29987A* (F). Monte Virgen, *Steyermark 42592* (F), *42603* (F, US).

HONDURAS. CHOLUTECA: Vic. of San Marcos de Colón, *Standley 15960* (F). COMAYAGUA: Siguatepeque, *Hazlett 649* (MO). Valibrea, *Rodríguez 2754* (F). Trincheras, *Williams & Molina 12538* (F, GH), *14661* (F, GH, MO, US). 20 km N of Siguatepeque, *Williams & Williams 18425* (GH, ISC). COPÁN: 5 km SE of Santa Rosa de Copán, *Molina 11667* (US). CORTES: Mont. La Cumbre, *Molina 10566* (US). N side of Lago Yojoa, *Morton 7633* (US). DISTRITO CENTRAL: Llamapa, *Pohl & Gabel 13525* (MO). EL PARAÍSO: Mt. Yuscaran, *Molina 620* (F, GH, MO, US). 7 km NW of San Lucas, *Pohl & Davidse 12161* (MO). Güinope, *Rodríguez 1761* (F). INTIBUCA: Vic. of La Esperanza and Intibuca, *Standley 25266* (F). MORAZÁN: Mt. Uyuca, *Davidse & Pohl 2098* (ISC, MO). 10 km NE of Tegucigalpa, *Davidse & Pohl 2119* (ISC). Between San Juancito and Valle de Angeles, *Davidse & Pohl 2126* (ISC, MO). Vic. of El Zamorano, *Freytag 224* (MO), *319* (MO). Mt. Uyuca, *Glassman 1947* (NY, WIS); *Molina 1432* (F, GH, US). 20 km S of Tegucigalpa, *Molina 18494* (F, GH, NY). Mt. Uyuca, *Standley 14063* (F), *20591* (F), *23103* (F, GH, MO, UC, US). El Jicarito, *Standley 26837* (F, GH, US). Mt. Uyuca, *Swallen 10904* (US). San Antonio de Oriente, *Swallen 10973* (US). Mt. Uyuca, *Williams & Molina 10722* (F, GH, MEXU, MO),

12113 (US). SANTA BARBARA: Near El Mochito, *Davidse & Pohl 2209* (ISC, MO). Above El Sauce, *Williams & Molina 14517* (F, GH, US).

MEXICO. CHIAPAS: Km 1134, Pan American Hwy., *Baldwin 14342* (US). Ala Shashib River, *Breedlove 6428* (F). La Trinitaria, *Breedlove 10056* (F, MEXU). Kulak'tik, Tenejapa, *Breedlove 10971* (F, MEXU). 17 mi E of La Trinitaria, *Breedlove 11322* (F). Zinacantán, *Breedlove 11827* (MEXU). 3 mi S of Aguacatenango, *Breedlove & Raven 13121* (NY). 19 km N of Ocozocoautla, *Breedlove 13956* (UC). 6–8 km N of Berriozábal, *Breedlove 20352* (MO). 18–20 km N of Ocozocoautla, *Breedlove & Thorne 21064* (MO). 13 km N of Berriozábal, *Breedlove 26303* (MO). Above El Chorreadero, *Breedlove 26857* (MO). 16 km NW of Rizo de Oro, *Breedlove 27616* (MO). 10 km SW of Ocosingo, *Breedlove 27859* (MO). 6–8 km N of Ocosingo, *Breedlove 27985* (MO). 18–20 km N of Ocozocoautla, *Breedlove 28156* (MO). 30 km NW of Ocozocoautla, *Breedlove 28907* (MO). 20 km S of Ocozocoautla, *Breedlove 29088* (MO). Above Talquian, *Breedlove 29477* (MO). 3 km E of Francisco Madero, *Breedlove 36679* (MO). 5 km W of Rizo de Oro, *Breedlove 36704* (MO). 3 km E of Francisco Madero, *Breedlove 38046* (MO). 14 km N of Tuxtla Gutiérrez, *Brunken & Perino 328* (MO). 30 km W of San Cristóbal, *Brunken & Perino 348* (MO). 36 km W of Tuxtla Gutiérrez, *Davidse & Davidse 9471* (MO). N of Tuxtla Gutiérrez, *Fassett 29100* (US). Zinacantán, *Laughlin 1218* (NY), *2094* (WIS), *2289* (F). Mt. Ovando, *Matuda 3987* (GH, MEXU, MO, NY). Zacatonal, *Matuda 18327* (MEXU, US). Berriozábal, *Miranda 6475* (US). 15 mi S of Comitán, *Reeder & Reeder 2094* (GH). 20 mi E of Chiapa de Corzo, *Reeder & Reeder 2127* (US). Near Mastepec, *Tateoka 1003* (US). N of Tuxtla Gutiérrez, *Tateoka 1004* (US). 125 km NE of Tuxtla Gutiérrez, *Tillett 636-57* (US). Mahosik, Tenejapa, *Ton 1133* (NY). Tih Ha', Tenejapa, *Ton 1446* (F, NY). Oshewits, Tenejapa, *Ton 1582* (NY). Between Escuipulas and Canada Honda, *Xolocotzi X-331* (US). Near El Triumfo, *Xolocotzi X-459* (US). GUANAJUATO: 2–4 km E of Guanajuato, *Sohns 286* (US). GUERRERO: Acapulco, *Cantú 16* (MEXU). Mancho Mina, *Hinton 9581* (MO, NY). Chilacayote-Mangito, Mina, *Hinton 14932* (GH, NY, US). W of Chilpancingo, *Sharp 441400* (MEXU, US). HIDALGO: Molango, *Moore 1951* (US). Between Pachuca and Zacualtipán, *Moore & Wood 4235* (US). Puerto del Zopilote, *Moore 5076* (GH, UC, US). JALISCO: San Nicolás, *Hitchcock 7207* (US). Guadalajara, *Hitchcock 7348* (US); *Jones 27614* (MO, NY, UC). Near El Molino, *McVaugh 13306* (US). 9 mi S of Autlán, *McVaugh 14232* (MEXU, US). 20 mi N of Tepatitlán, *McVaugh 17363* (NY, US). Barranca Ibarra, *Reko 4561* (MEXU), *4563* (MEXU). El Molino, *Rzedowski 14254* (US). MÉXICO: Near Villa Guerrero, *Alexander & Hernández 1908* (NY). Temascaltepec, *Hinton 1909* (GH, NY, US). Tejupilco, *Hinton 4958* (MEXU, NY). Temascaltepec, *Hinton 6722* (ISC, MO, NY, US); *Matuda 26610* (MEXU, US). Jilotepec, *Matuda 26752* (MEXU). Ixtapan de la Sal, *Matuda 27046* (MEXU). 9 km N of Ixtapan, *Roe & Roe 1853* (MEXU, WIS). 2 km N of Ixtapan, *Roe & Roe 1903* (MEXU, WIS). MICHOCÁN: Vic. of Morelia, *Arsène 2703* (P), *2976* (MO, US), *5287* (MO, US), *6096* (P), *8487* (MO, US), *8700* (US). 1.2 mi E of Tuxpan, *Brunken & Perino 440* (MO). Ca. 1.7 mi NW of Tuxpan, *Davidse & Davidse 9819* (MO). Apatzingan, *Hinton 15156* (GH, NY, US). 22 km S of Uruapan, *King & Soderstrom 4813* (MEXU, NY, UC, US). 1 km below Tacambaro, *Moore et al. 5598* (GH, UC, US). MORELOS: Near Guernavaca, *Leavenworth & Leavenworth 927* (F, MO). Teposteco, *Lyonnet 1373* (US), *2541* (US). Near Guernavaca, *Lyonnet 2827* (US); *Pringle 5960* (ISC, MEXU, US), *6663* (F, GH, GOET, ISC, M, MO, NY, P, UC, US). Near Tepoztlan, *Seler 4292* (GH, US). NAYARIT: 10 km S of Compostela, *Rzedowski 14359* (MEXU). NUEVO LEÓN: Between Potrero Redondo and Las Ajuntas, *Muller 2961* (F, GH, MO, UC, US). OAXACA: 15 km WSW of Oaxaca, *Camp 2461* (MO, NY). Ca. 10 km NE of Oaxaca, *Conrad & Conrad 3064* (MO). Cerro San Antonio, *Conzatti 1596* (F). San Pablo Heintzo, *Conzatti 2012* (F, MEXU, US). Vic. of Oaxaca, *Kenoyer 1547* (GH). Tomellin Canyon, *Pringle 6701* (F, GH, GOET, ISC, M, MEXU, MO, NY, P, UC, US). Cafetal Montecristo, *Reko 3474* (MEXU, US). PUEBLA: La Mesa Necaxa, *Miranda 4125* (MEXU). Hacienda de Noria, *Nicolás s.n.* (P). El Cerro de Chuhuatepetl, *Santos 3347* (US). Between Puebla and Atlixco, *Sharp 44943* (MEXU, US). SAN LUIS POTOSÍ: 34 mi E of San Luis Potosí, *Johnston & Crutchfield 6028* (US). Las Canoas, *Pringle 3808* (F, GH, GOET, ISC, MEXU, MO, NY, P, UC, US). Minas de San Rafael, *Purpus 5439* (UC, US). 41 mi E of San Luis Potosí, *Reeder & Reeder 4765* (US). 13 km W of Santa Catarina, *Roe & Roe 2207* (MEXU, WIS). Sierra de Alvarez, *Sohns 1198* (US). Sierra de Guadalcazar, *Sohns 1378* (US). Sierra de Alvarez, *Sohns 1390* (US). To Xilitla, *Sohns 1437* (US). TAMAULIPAS: 22 km SE of Miquihuana, *Stanford et al. 870* (GH, MO, NY). To Piña Nevada, *Stanford et al. 2502* (US). VERACRUZ: Orizaba, *Balls B4294* (UC, US). Coapepec, *Baldwin 14270* (US). 15 mi SE of Xalapa, *Barkley et al. 2594* (F), *2597*

(F). Jalapa, *Beetle M-2216* (MO, WIS). 3 km SW of Orizaba, *Croat 39510* (MO). Córdoba, *Fisher 35298* (F, MO, NY); *Hitchcock A.G.N.H.409* (F, GH, MO, NY, UC, US). Orizaba, *Hitchcock A.G.N.H.415* (F, GH, MO, NY, US), *6389* (US). Córdoba, *Hitchcock 6393* (US), *6442* (US), *6445* (US), *6458* (US). Jalapa, *Hitchcock 6642* (US), *6674* (NY, US), *6680* (US). Near Mirador, *Hohenacker 9* (GOET), *9a* (GOET, P), *9c* (GOET). El Plan de Las Hayas, *Lot 444* (GH). Jalapa, *MacDaniels 857* (F). Zacuapan, *Purpus 3779* (F, GH, NY, US), *6205* (UC, US). Cerro Macuiltepec, *Reeder & Reeder 5984* (MO). Jalapa, *Rose & Hay 6144* (MEXU, NY, US). Near San Martin, *Rozynski 589* (F, NY). 30 km NW of Zongolica, *Santos 3076* (NY, US). Orizaba, *Seaton 393* (F, GH, NY, US). Near Río Blanco, *Sharp 44885* (MEXU, US). Orizaba, *Smith 581* (US). 5 km N of Jalapa, *Weaver 908* (UC).

NICARAGUA. CARAZO: Jinotepe, *Hitchcock 8865* (US). JINOTEGA: La Bastilla, *Seymour 2120* (F, GH, MO). Cerro Sialci, *Standley 10467* (F). MANAGUA: El Crucero, *Atwood & Neill 6753* (MO). Sierra de Managua, *Garnier A-1243* (F, GH, US), *1533* (GH), *1549* (GH, US); *Maxon et al. 7514* (GH, US). Ca. 5.4 km NE of El Crucero, *Stevens 5810* (MO). MATAGALPA: Between Matagalpa and Jinotega, *Williams et al. 23316* (F, NY, US), *23340* (F, NY, US). 6 km NE of Matagalpa, *Williams et al. 24032* (F, NY, US).

PANAMA. CHIRIQUÍ: Boquete, *D'Arcy 9849* (MO). E slope of Volcán Chiriquí, *Davidse & D'Arcy 10155* (MO). Vic. of Boquete, *Davidson 710* (F, GH, MO, US). Between Boquete and Cerro Horquete, *Duke A13704* (MO, UC). Vic. of Boquete, *Hitchcock 8269* (US), *8270* (GH, NY, US), *8282* (US), *8286* (US), *8311* (US), *8315* (US); *Killip 4544* (US); *Lewis et al. 569* (F, GH, MO, NY, UC, US). Cerro Vaca, *Pittier 5331* (GH, NY, US). COCLÉ: 5 mi W of El Valle, *Hammel 1765* (MO). PANAMÁ: Cerro Campana, *Duke 8698* (MO).

VENEZUELA. ARAGUA: Rancho Grande, *Davidse 3033* (ISC, MO). Alto de Choroní, *Davidse 3100* (ISC, MO). Vic. of Colonia Tovar, *Fendler 1619* (GH, MO). Alto de Choroní, *Soderstrom 974* (US, VEN). Parque Nacional Henri Pittier, *Soderstrom 1357* (US). Carretera Maracay-Choroní, *Trujillo 9146* (MY). Vic. of Colonia Tovar, *Woronow 7295* (US). BOLÍVAR: Mission Santa Teresito de Kavanayen, *Maguire & Wurdack 33758* (F, NY, US, VEN). DISTRITO FEDERAL: Between Caracas and La Guiara, *Burkhart 17001* (VEN). Cotiza, *Chase 12408* (US). Between El Junquito and Tovar, *Davidse & Morillo 3999* (MO); *Davidse 4032* (MO). Los Venador, *Lasser 996* (VEN). Near Agua Negra, *Pittier 13739* (VEN). El Junquito, *Schnee 498* (NY). Above Caracas, *Steyermark 55106* (F, US). Cerro Naiguatá, *Steyermark 92125* (US, VEN). MÉRIDA: 35 km W of Mérida, *Breteler 3124* (VEN). 66 km NE of Mérida, *Davidse 3240* (ISC, MO). Tabay, *Gehringer 398* (F, NY, US, VEN). La Mucuy, *Oberwinkler 13261* (M). Above La Azulita, *Steyermark 56098* (F, US, VEN). MIRANDA: Between Las Canales and El Encanto, *Lasser 665* (VEN). El Avila, *Morillo & Manare 1586* (VEN). SUCRE: Las Altas, *Tamayo 2125* (US). TRUJILLO: 16 km from Boconó, *Breteler 4088* (US). 34 km from Valera, *Breteler 4136* (US). ZULIA: Periva, *Gines 2034* (VEN).

SMALL-SPIKELET FORM OF *L. NIGRA*

COLOMBIA. CHOCÓ: Alrededores de San José del Palmar, *Forero & Jaramillo 2468* (MO). Carretera Ansermanuevo-San José del Palmar, *Forero et al. 2231* (MO), *2922* (MO). MAGDALENA: Sierra de Santa Marta, *Kirkbride 2223* (MO).

COSTA RICA. CARTAGO: 3–5 km from Moravia, *Croat 36611* (MO). 7 km W of Turrialba, *Croat 36842* (MO). 5 km SW of Tapantí, *Taylor & Taylor 4471* (MO). Above Platanillo, *Wilbur & Stone 10620* (MO). PUNTARENAS: Río Coto Brus, *Croat 26615* (MO). Monteverde, *Pohl & Pinette 13250* (MO). Ca. 6 km SE of San Vito de Java, *Pohl & Pinette 13275* (MO).

GUATEMALA. ALTA VERAPAZ: 2–3 mi S of Purulha, *Croat 41728* (MO).

HONDURAS. OCOTEPEQUE: 20 km from Nueva Ocotepeque, *Molina 22361* (F, MO).

MEXICO. CHIAPAS: Ca. 8 mi NE of Solistohuacan, *Davidse & Davidse 9458* (MO).

NICARAGUA. JINOTEGA: Ca. 5–8 mi SW of Jinotega, *Croat 43048* (MO).

PANAMA. CHIRIQUÍ: N of San Felix, *Mori & Kallunki 5916* (MO). COCLÉ: Ca. 3 km N of El Valle, *Mori & Kallunki 2944* (MO). DARIÉN: Cerro Sapo, *Hammel 1209* (MO). VERAGUAS: 7 km NW on rd. to Santa Fé, *D'Arcy 10258* (MO). Río Segundo Brazo, *Maas & Dressler 1635* (MO). Cerro Tute, *Witherspoon et al. 8866* (ISC, MO).

VENEZUELA. ARAGUA: Rancho Grande, *Davidse 3038* (ISC, MO, VEN).

8a. **Lasiacis oaxacensis** (Steud.) Hitchc. var. **oaxacensis**, Proc. Biol. Soc. Wash. 24: 45. 1911.

Panicum oaxacense Steud., Syn. Pl. Glum. 1: 73. 1854. TYPE: Mexico, Oaxaca, *Lenormand s.n.* (P, holotype, photograph US, fragment US).

Perennial; culms rather coarse, extensively creeping and rooting at the nodes, the ultimate parts more or less erect, 0.5–2.0 m tall, highly branched; internodes 2–5 mm thick, solid, rarely partially hollow, glabrous, mostly herbaceous; nodes glabrous; sheaths glabrous, rarely somewhat puberulent on young leaves, one or both margins usually ciliate, if both margins ciliate, then the inner one ciliate only near the apex, occasionally both glabrous; collar often densely puberulent or pubescent along the margins, with hairs 0.5–2.0 mm long, sometimes puberulent or pubescent on the back, or completely glabrous; ligule prominent, (2.0–)2.6–5.0(–6.0) mm long, brown, usually appressed puberulent or hispid on the back, the margins ciliate with hairs to 2 mm long, or glabrous, the apex ciliate and usually lacerate; blades (13–)17–29 cm long, 1.2–2.4 cm wide, narrowly linear-lanceolate, glabrous and usually conspicuously scabrous especially along the midribs, rarely puberulent when young, the margins scabrid, the base nearly symmetrical, the apex acuminate; panicles mostly terminal, 16–31 cm long, the longest branch (4–)9–18(–24) cm long, the branches widely spreading, mostly naked on the lower ½ or ⅔, bearing pedicellate spikelets in pairs or small clusters toward the ends of the branchlets; spikelets mostly 3.8–4.2 mm long; first glume 1.6–2.3 mm long, 4–6-nerved; second glume 7–11-nerved; sterile floret usually bearing a staminate flower and then possessing well-developed lodicules, the sterile palea as long as the fertile floret, the anthers 1.0–2.3 mm long, occasionally reduced to rudiments; fertile floret 3.2–3.6 mm long, 1.9–2.3 mm wide, the anthers 1.7–2.3 mm long, the stigmas purple; caryopsis 2.0 mm long, 1.6 mm wide; chromosome number $n = 18$.

Ecology: *Lasiacis oaxacensis* var. *oaxacensis* characteristically occurs along forest edges, in open places in forests and thickets, along fence rows in plantations, and shrubby road embankments. Label data from *Popenoe 15* reported that in low elevations in Guatemala, it may become prominent in cultivated fields six months after abandonment. Similar observations are reported by Johnston (1949) for San José Island, in the Pearl Islands south of Panama. There this species became very common along roadsides and trails through the forest and thickets as a result of the disturbance caused in the vegetation by U.S. forces during World War II. Subsequently abandoned areas became choked with large tangles of this species.

Variety *oaxacensis* has been collected primarily at elevations ranging from sea level to 1,600 m. The majority of flowering specimens have been collected from November to April. A number of flowering specimens from Ecuador and Peru were collected in May to October.

Distribution: *Lasiacis oaxacensis* var. *oaxacensis* is distributed in Mexico from Nayarit, south to Guerrero, eastward to Veracruz, and then south throughout Central America. I have not seen any specimens from Michoacán. In South America, it occurs in Colombia (infrequently), Venezuela, and south to Ecuador and Peru. It has also been collected in Jamaica and Hispaniola in the West Indies.

Lasiacis oaxacensis var. *oaxacensis* is characterized by its solid, procumbent culms which bear long, relatively narrow leaves that have prominent ligules and glabrous sheaths. It forms open panicles with spreading branches which bear spikelets, often in pairs or small clusters, toward the tips of the branches. The sterile palea is as long or nearly as long as the fertile lemma, and the sterile floret usually has a staminate flower. There are three collections known to me from Ecuador that do not have the solid pith, characteristic of specimens from all other areas.

Lasiacis oaxacensis is a distinctive species most closely related to *L. linearis*. The main differences between these two are discussed under the latter species. Occasional herbarium specimens representing very young plants or old, highly branched plants approach *L. standleyi* in gross appearance. However, the solid culms and more distally borne spikelets with well-developed sterile paleas reliably distinguish *L. oaxacensis*.

In occasional specimens, some of the lateral veins of the first glume may be partially or completely suppressed giving this bract a 4- or 5-nerved appearance. Such suppression may happen in any spikelet bract in any species but is perhaps somewhat more frequent in this species.

Sousa 525 from Oaxaca, Mexico, and *Davidse & Pohl 2205* from Atlantida, Honduras, are unusual in that the inflorescences contain a number of spikelets with extra fertile or sterile florets. Although the occurrence of an extra sterile lemma characterizes *L. anomala*, the presence of an extra fertile or sterile floret is known only in hybrids (unpublished). This means that the possibility of hybridization must be considered for these two collections. The Sousa specimen (MEXU) is quite fragmentary, being composed of only one inflorescence and one leaf. On the basis of the leaf, the specimen falls well within the range of *L. oaxacensis*. The inflorescence is more highly branched than is usual for *L. oaxacensis*. The evidence is not conclusive, and the unusual nature is simply noted. In the Honduranian collection, 16% of a random sample of 100 spikelets from two different inflorescences had an extra fertile or sterile floret. Some of the larger leaf blades were up to 2.7 cm in width, wider than in any specimen of *L. oaxacensis*, and the basal segments were ciliate. Blades on secondary branches were smaller. Inflorescences were also more densely branched than usual. The culms were hollow but were lined with a definite layer of pith. All these features suggest a hybrid plant. Pollen stainability was determined to be approximately 40% on the basis of samples from herbarium specimens. The anthers I used came from spikelets that had opened and begun to exsert stigmas and stamens, although none of the anthers showed dehiscence. Since anther indehiscence is characteristic of many known hybrids (unpublished), this is another indication that the plant may be of hybrid origin. *Lasiacis oaxacensis* would be one parent. The second one is unknown, but the ciliate leaf base of the putative hybrid suggests *L. procerrima* or *L. ruscifolia*, two common *Lasiacis* species with this character.

Common names: The following common names have been reported; Mexico: Oaxaca: zacate de escobe, *Sousa* 525. British Honduras: rat rice, *Gentle* 3937.

Ecuador: Chimborazo: tundilla, *Solís 5176*. Los Ríos: paja de saino, *Solís 19481*.

BELIZE. BELIZE: Gracie Rock, *Lundell 1769* (MEXU, MO, NY), *6942* (US). STANN CREEK: Near Hope Creek, *Gentle 7874* (IJ, NY, UC, US). Stann Creek Valley, *Gentle 9088* (F, US). TOLEDO: Monkey River, *Gentle 3937* (F, GH, MO, NY, US). Beyond Columbia, *Gentle 6172* (GH, IJ). Crique Negro, *Gentle 7205* (IJ, NY, UC, US).

COLOMBIA. MAGADALENA: Santa Marta, *Smith 2142* (COL, F, GH, ISC, MO, NY, P, US, WIS).

COSTA RICA. ALAJUELA: Carrillos de Alajuela, *Brenes 17380* (F, NY), *17439* (F, NY). 4 km W of Alajuela, *Pohl 12545* (ISC). GUANACASTE: Orillas del Río Bebedero, *Jiménez 724* (US). Río Naranjo, *Pohl & Lucas 13059* (MO). El Arenal, *Standley & Valerio 45151* (US). LIMÓN: Guápiles, *McKee 11101* (P). PUNTARENAS: 12 km SE ot Paso Real Ferry, *Pohl & Lucas 13121* (MO). SAN JOSÉ: San José, *Hitchcock 8488* (US), *8496* (US). Vic. of El General, *Skutch 3821* (GH, MO, NY, US), *3863* (GH, NY, US).

DOMINICAN REPUBLIC. SAMANÁ: Vic. of Sánchez, *Abbott 180* (US).

ECUADOR. CAÑAR: Río Yaguachi, *Valer 178* (MO). CHIMBORAZO: Bucay, *Solís 5176* (F, US). ESMERALDAS: Between Santo Domingo de los Colorados and Quinindé, *Asplund 16365* (US). GUAYAS: Los Alamos, *Anderson 524* (UC). Recreo, *Eggers 15572* (P, US). Milagro, *Hitchcock 20299* (F, GH, NY). LOS RÍOS: Pichilingue, *Solís 10703* (F, US), *19481* (US). PROVINCE UNKNOWN: Vic. of Ventura, *Rose & Rose 23525* (GH, NY).

EL SALVADOR. LA LIBERTAD: Santo Tomás, *Calderón 1922* (MO). Volcán San Salvador, *Davidse & Pohl 2026* (ISC); *Fassett 28590* (F, GH, US, WIS). 5 km S of Santa Tecla, *Williams & Molina 15089* (US). MORAZÁN: Montes de Cacaquatique, *Tucker 694* (F, ISC, US).

GUATEMALA. ALTA VERAPAZ: Cubilqüitz, *von Tuerckheim 7701* (US). GUATEMALA: Guatemala City, *Hitchcock 9045* (US), *9080* (US), *9107* (US). Villalobos River, *Molina et al. 16075* (F, NY). N of Guatemala City, *Popenoe 735* (US). Barranca de las Vacas, *Standley 59537* (F). Near Amatitlán, *Standley 61399* (F, US). IZABAL: Between Los Amates and Izabal, *Kellerman 7486* (NY). Murciélago, *Popenoe 15* (F). Vic. of Quirigua, *Standley 24122* (GH, NY, US). Between Milla 49.5 and Cristina, *Steyermark 38669* (F). Quirigua, *Weatherwax 17* (US), *81* (US). JUTIAPA: Between Jutiapa and La Calera, *Standley 76153* (F). QUEZALTENANGO: Near El Muro, *Standley 67236* (F). RETALHULEU: Retalhuleu, *Kellerman 6273* (F, US). E of Chivolandia, *Standley 67051* (F). SACATÉQUEZ: Near Las Lajas, *Standley 58104* (F, US). Volcán del Fuego, *Standley 60256* (F). SANTA ROSA: Near Oratorio, *Standley 60645* (F). Near Cuilapa, *Standley 77695* (F). SE of Barberena, *Standley 77791* (F).

HAITI. L'ARTIBONITE: Kalacroix, *Leonard 7997* (US). NORD: Bayeux, *Ekman 2841* (IJ, US). Vic. of Marmelade, *Leonard 8192* (F, MO, US). Vic. of Dondon, *Leonard 8572* (IJ, NY, US). Plaisance, *Leonard 9391* (GH, UC, US). SUD: Massif de la Hatte, *Ekman 7153* (GH, IJ, US).

HONDURAS. ATLANTIDA: Between Tela and Pajuiles, *Molina & Molina 25714* (F, NY). Vic. of Tela, *Standley 54543* (F, GH, US). Vic. of San Alejo, *Standley 7648* (F). MORAZÁN: 12 km E of El Zamorano, *Davidse & Pohl 2127* (ISC). Vic. of Tegucigalpa, *Standley 24910* (F, NY, UC). SANTA BÁRBARA: 1 km de Santa Bárbara, *Molina 3676* (F, GH, US).

JAMAICA. CLARENDON: Peckhaus, *Harris 12828* (F, GH, MO, NY, US). PORTLAND: Nanny Town site, *Morley & Whitefoord 490* (MO). ST. ANN: Mt. Diablo, *Hunnewell 15225* (IJ). ST. CATHERINE: *Rothrock 302* (F). ST. THOMAS: Port Morant, *Rothrock s.n.* (F, NY). TRELAWNY: Near Troy, *Hitchcock 9800* (US). WESTMORLAND: Lindo's Hill, *Harris 11832* (F, GH, MO, NY, P, US).

MEXICO. CHIAPAS: 17 km N of Tuxtla Gutiérrez, *Breedlove 13903* (F). 10 km SE of Mapastepec, *Breedlove & Thorne 30726* (MO). W side of Laguna Miramar, *Breedlove 33325* (MO). Zacualpa, *Juzepczuk 1275* (US). Jilquero, *Matuda 17286* (F, MEXU, NY). Aguas Calientes, *Miranda 1788* (MEXU). San Quentin, *Sohns 1685* (MEXU). GUERRERO: Sierra Madre, *Langlassé 556* (GH). JALISCO: 2 mi N of La Cuesta, *McVaugh 21157* (NY, UC). NAYARIT: 9 mi N of Compostela, *McVaugh & Koelz 510* (NY, US). OAXACA: Chiltepec, *Martínez-Calderón 483* (GH, UC, US). 1 km N of Tolosito, *Pohl & Davidse 11818* (ISC). Temascal, *Sousa 525* (MEXU), *1067* (MEXU). VERACRUZ: Valle de Córdoba, *Bourgeau 1461* (GH, P). Pital, *Liebman N-285* (MO). Hidalgotitlan, *Dorantes 3750* (MO). Zacuapan, *Purpus 2157* (F, MO, NY, UC). S del Volcán San Martin, *Sousa 2218* (MEXU). Fortuño, *Williams 8271* (F, P, US), *8654* (F).

NICARAGUA. CARAZO: Jinotepe, *Hitchcock 8672* (UC, US), *8698* (US). MANAGUA: Sierra de Managua, *Garnier 27* (US), *39* (US), *1557* (GH). ZELAYA: Río Grande, *Molina 2503* (F).

PANAMA. BOCAS DEL TORO: Almirante, *Cooper 105* (US). Vic. of Chiriquí Lagoon, *von Wedel 2086* (GH, MO, US). CANAL ZONE: Albrook Forest, *Blum 2089* (MO, SCZ). Barro Colorado Island, *Croat 7081* (MO), *7473* (MO), *7730* (MO), *13115* (MO). Gatún Lake, *Hitchcock A.G.N.H.412* (F, GH, NY, P, UC, US). Vic. of Frijoles, *Killip 4284* (US). Darién, *Killip 4306* (US). Empire to Mandinga, *Killip 5278* (US). Agua Clara Reservoir, *Maxon 4653* (GH, US). 7.5 km SW of the Gatún Dam, *Nee & Gentry 8671* (MO). Near Culebra, *Standley 26009* (MO, US). Vic. of Frijoles, *Standley 27410* (US). Gamboa, *Standley 28535* (US). Vic. of Gatún Lake Dam, *Tyson & Blum 1998* (MO). Curundu, *Tyson & Blum 2531* (MO). CHIRIQUÍ: Burica Peninsula, *Croat 22553A* (MO); *Liesner 64* (MO). COLÓN: 4 km ENE of Buena Vista, *Nee 9124* (MO). Between France Field and Cativa1, *Standley 30230* (US). DARIÉN: Río Chico, *Duke & Bristan 437* (MO). Río Chucanaque, *Duke 5107A* (MO). HERRERA: Río Guacino, *McCorkle C-126* (SCZ). PANAMÁ: San José Island, *Erlanson 308* (GH, NY, US); *Johnston 681* (GH), *904* (GH, US), *1032* (GH). 3 km S of Alcalde Diaz, *Nee 8853* (MO). Juan Diaz, *Standley 30591* (US). San José Island, *Tyson & Loftin 5061* (MO), *5070* (MO, SCZ).

PERU. HUÁNUCO: Tingo Maria, *Asplund 12197* (US). JUNÍN: Río Perenne, *Killip & Smith 25170* (NY, US). LORETO: Below Tabacoas, *Anderson 1018* (UC, US). SAN MARTIN: Quebrada de Huaquisha, *Schunke 7001* (MO). 3–4 km de San Juan de Pacaizapa, *Schunke 9758* (MO).

VENEZUELA. ARAGUA: Rancho Grande, *Box 3957* (MY, VEN); *Davidse 3113* (ISC, MO), *4980* (ISC, MO). Guamitos, *Pittier 15209* (US, VEN); *Tamayo 705* (VEN). MÉRIDA: Tycoporo Forest Reserve, *Breteler 3443* (COL, NY, VEN). MIRANDA: Parque Nacional Guatopo, *Croat 21700* (MO). SUCRE: Cumanacoa, *Pittier 14675* (VEN). YARACUY: Colonia El Gayobo, *Aristeguieta & Foldats 1253* (VEN).

8b. **Lasiacis oaxacensis** (Steud.) Hitchc. var. **maxoni** (Swallen) Davidse, Ann. Missouri Bot. Gard. 64: 375. 1978.

Lasiacis maxoni Swallen, Ann. Missouri Bot. Gard. 30: 231. 1943. TYPE: Panama, Chiriquí, vicinity of El Boquete, in thickets along wet trail, 1000–1300 m, 2–8 Mar. 1911, *Maxon 4999* (US, holotype; US, isotype).

Similar in aspect to *L. oaxacensis* var. *oaxacensis*; culms glabrous, solid; sheaths glabrous; collar glabrous, puberulent, or puberulent only on the margins; ligule 0.5–1.5 mm, the apex minutely ciliolate, or ciliate with hairs 1.0 mm long, tan, ciliate on the margin; blades 16–25 cm long; longest panicle branch 11–22 cm long; spikelets clearly paired near the tips of the branchlets, 3.7–4.0 mm long; first glume 1.6–2.3 mm long; sterile palea equal or nearly so to the fertile floret; sterile floret with a staminate flower; chromosome number $n = 18$.

Ecology: This variety is ecologically similar to var. *oaxacensis* in growing along forest edges, thickets, and in cleared areas as a pioneer species at elevations ranging from 800 to 1,300 m. Flowering specimens have been collected primarily from October to January, although a Honduran collection has been made in June.

Distribution: *Lasiacis oaxacensis* var. *maxoni* is known from Panama to Nicaragua.

Swallen (1943) described *L. maxoni* without differential diagnosis or discussion. In the key to Panamanian species, he used the following characters to distinguish this species from related ones: "Ligule 0.5–1.0 mm long, pale, truncate; panicles loosely flowered, the spikelets in pairs at the ends of branches

and branchlets." In panicle characteristics var. *maxoni* is identical with may specimens of var. *oaxacensis*, including the holotype. The range of variation is, however, much greater in var. *oaxacensis*. Of the two key characters, var. *maxoni* is only differentiated from *L. oaxacensis* by the short ligules. Even in this character, however, a greater range of variation has been discovered since Swallen's treatment. A number of specimens with ligule size ranging between 1 and 2 mm are now known, thus partially bridging the morphological distinction between these two taxa. Since there is no correlation with other characters, I prefer to reduce *L. maxoni* to infraspecific status.

COSTA RICA. ALAJUELA: Alajuela, *Jiménez 152* (US). 1.5 km S of San Pedro de Poás, *Pohl & Davidse 11522* (ISC). CARTAGO: Tucurrique, *Tonduz 12858* (NY). GUANACASTE: Vic. of Tilarán, *Standley & Valerio 44523* (US). SAN JOSÉ: San Pedro, *Greenman & Greenman 5289* (MO, US). Llano Grande de Puriscal, *Jiménez 887* (US). Vic. of El General, *Skutch 2226* (GH, MO, NY, US). San Francisco de Guadelupe, *Tonduz 7199* (US), *9818* (ISC).

HONDURAS. EL PARAÍSO: Agua Fria, *Molina 11338* (UC). YORO: 15 km SSE of Río Viejo, *Davidse & Pohl 2199* (ISC).

NICARAGUA. MATAGALPA: Santa Maria de Ostuma, *Williams et al. 24776* (F).

PANAMA. CHIRIQUÍ: Vic. of Boquete, *Hitchcock 8281* (US). Between Flato del Jobo and Cerro Vaca, *Pittier 5422* (US). COCLÉ: El Valle de Antón, *Dwyer 11842* (MO); *Dwyer & Nee 11942A* (MO); *Lewis et al. 2594* (COL, MO, UC).

9. **Lasiacis procerrima** (Hack.) Hitchc., Proc. Biol. Soc. Wash. 24: 145. 1911.

Panicum procerrimum Hack., Oesterr. Bot. Z. 51: 431. 1901. TYPE: Costa Rica, inter frutices ad flavium Tilirí prope La Verbena et Alajuelita, 1000 m, Aug. 1894, *Pittier 8819* (W, holotype, photograph US; US, isotype).

Short-lived perennial or annual; conspicuous unbranched, adventitious prop roots at the lower, usually decumbent nodes; culms in clumps, rarely simple, decumbent at base, (0.5–)1.0–4.0(–5.0) m long, simple or sparingly branched from the upper and middle nodes, hollow, 4–10(–12) mm thick, glabrous or occasionally puberulent below the nodes, herbaceous to lignified; nodes glabrous; sheaths glabrous or puberulent and glaucous, occasionally hispid, rarely short woolly, the overlapping sheath margin ciliate near the apex with hairs 1.5–2.5 mm long or sometimes entirely glabrous; sheath auricles, if present, up to 2.0 mm long, often pubescent and ciliate; collar glabrous to puberulent; ligule 0.5–1.5(–2.1) mm long, usually glabrous and minutely ciliolate, occasionally puberulent on the back; leaf blades linear-lanceolate or lanceolate (14–)18–35 (–42) cm long, (1.4–)1.8–4.8(–5.7) cm wide, usually broadest just above the base, usually glabrous, hispidulous, or minutely velutinous and conspicuously glaucous on the lower surface, rarely hispid with hairs to 3.0 mm long, the apex acuminate, the base conspicuously cordate, clasping the stem, the basal segments conspicuously ciliated with hairs 1.5–2.5 mm long, or glabrous, the margin scabrid; panicles large, highly branched and diffuse, (20–)32–120 cm long, about as wide, the peduncle exserted, glabrous, the branches tending to be whorled toward the base, scabrous, bearing a few widely spaced sessile or short-pedicelled spikelets on the distal ¼ or ⅙, the pulvini glabrous, rarely puberulent; spikelets (3.0–)3.5–4.0(–4.8) mm long; first glume (1.4–)1.6–2.1(–3.0) mm long, 7–11-nerved; second glume 9–11-nerved; sterile floret usually with a well-developed

staminate flower, or rarely with a perfect flower, the stamens 1.8 mm long, rarely rudimentary, the lemma 9–11-nerved, the palea ¾–⅚ the length of the fertile floret; fertile floret 3.1–3.4 mm long, 1.8–2.1 mm wide, black to grayish brown at maturity, the upper margin of the fertile lemma not inrolled, the anthers 1.6–1.9 mm long, yellowish, the stigmas white; caryopsis 2.3 mm long, 1.8 mm wide, dark brown; chromosome number $n = 18$.

Ecology: Very common on bare road embankments, also on partially wooded, brushy slopes in secondary associations, grassy slopes and thickets in open pine-oak forests, open savanna woodlands, wooded quebradas, and trails in montane forests. It has been collected up to 1,800 m. Spikelets are produced primarily from June to January.

Distribution: *Lasiacis procerrima* occurs in Mexico from Sinaloa and Durango to Puebla, south throughout Central America, across northern South America to Guyana, northern Brazil and south to central Peru.

Although Hackel (1901) cited the type collection as *Pittier 8819*, the two isotypes at US actually ascribe the collection to Tonduz, and the citation for the type collection based on these specimens is as follows: Costa Rica, Buissons au bord du Tilirí près La Verbena et Alajuelita, 1000 m, Aug. 1894, *Tonduz 8819*.

Lasiacis procerrima is the most distinctive species in the genus and is rarely misidentified. The very large leaves with prominent, clasping, basal lobes and the large diffuse panicles readily distinguishes it from all other American paniciod species. The lower branches of the inflorescence tend to become whorled, and in this it somewhat resembles *Panicum mertensii* Roth. The whorled condition is, however, much more regular and highly developed in *P. mertensii*. In *P. mertensii* panicle branches completely encircle the main inflorescence axis at the nodes, something which rarely happens in *L. procerrima*. *Panicum mertensii* can also be distinguished in that it lacks the cordate leaf bases, the large prop roots, and woolly pubescence of the spikelets. Soderstrom (pers. comm.) has suggested that this species may actually belong with *Lasiacis*. Hackel (1901), in the original description of *Panicum procerrimum*, also noted that his newly described species was closely related to *P. mertensii* (reported as *P. megiston* Schult.). This species resembles *Lasiacis* somewhat in that the somewhat globose spikelets tend to be borne obliquely on the pedicel. It differs in all the other spikelet characters by which *Lasiacis* is defined, namely the lack of woolly pubescence at the tips of the spikelet bracts, black spikelets at maturity, and the lack of gibbous-concave configuration of the fertile palea. Cytologically, Gould & Soderstrom (1970) reported *P. mertensii* to have the probable chromosome number $2n = 36$ based on a collection from Colombia. Later Pohl & Davidse (1971) reported the number to be $2n = 40$ from a Costa Rican locality. Since Gould felt his determination to be doubtful, it seems probable that the $2n = 40$ number is correct. Therefore, *P. mertensii* has the base number $x = 10$ whereas all species of *Lasiacis* chromosomally known have the base number $x = 9$. Thus, both on the basis of spikelet morphology and cytology, *P. mertensii* does not belong in the genus *Lasiacis*. Hitchcock & Chase (1910) considered *P. mertensii* (*P. megiston*) to be anomolous in the genus *Panicum*. I concur

with this point of view and feel that the unity of *Lasiacis* would be destroyed by the inclusion of *P. mertensii.*

Lasiacis procerrima commonly has glabrous, glaucous leaves; plants with pubescent leaves are less common. However, throughout Mexico and Central America, the alternatives: glabrous blades and puberulent sheaths or pubescent blades and glabrous sheaths can be found. This indicates that a number of gene loci are involved in pubescence characters and that segregation for these genes is taking place. Thus, considerable variation in pubescence is exhibited. The most extreme cases are the almost woolly sheaths of *Rodríguez 1865* (El Paraíso) and *Davidse & Pohl 2161* (Morazán) in south-central Honduras. Also notable are the hispid leaves of *Tyson 2103* (Canal Zone) and *Duke 8672* (Panamá) from central Panama. Another notable pattern of morphological variation is the widespread occurrence of plants with glabrous, glaucous leaves in South America.

Lasiacis procerrima normally has a few, well-separated sessile or short-pedicelled spikelets below the terminal spikelet. *Molina 228* from Morazán, Honduras, is unusual in having most of the spikelets conspicuously clustered in twos and threes at the ends of the inflorescence branches, a feature that often characterizes the inflorescence of *L. oaxacensis* and *L. rhizophora.* Another collection, *Davidse & Pohl 2081*, from Honduras shows an even more extreme condition of clustered spikelets. In some of the branches, the pedicels are so reduced that two or three spikelets have become united in one massive spikelet. This, coupled with the loss of some bracts of the spikelets, gives these spikelets a fascicled, abnormal appearance.

Unusually large spikelets (4.7 mm) occur in *Hinton 2408* from Temacaltepec, Mexico, and unusually large first glumes occur in *Mexia 628* (2.9 mm) from Nayarit, Mexico, and *Hitchcock 7085* (3.5 mm) from Colima, Mexico. These specimens are in all other respects typical representatives of this species.

Common names: The following vernacular names have been reported for *L. procerrima*: Mexico: Chiapas, zacatón, *Chavelas et al. 1649.* Oaxaca, cordoncilla, *Chavelas & Perez 6.* Puebla, zacatón, *Sarukhan et al. 1335.* Tabasco, zacate cenizo, *Dioscoreas 11507.* British Honduras: rat rice, *Gentle 3692*; water bamboo *Sinart 39.* Guatemala: Huehuetenango, cañuela, *Steyermark 49201.* Izabal, cola de venado, *Blake 7836.* El Salvador: San Salvador, carrizo de cohetes, *Calderón 849.* Costa Rica: Alajuela, cañuela, *Jiménez 532*; trompilla, *Jiménez 886.* Venezuela: Anzoátegui, pito-pito, *Steyermark 61115.* Colombia: Boyaca, cañuela, *Lawrance 795.*

Economic uses: *Steyermark 49201* reported on the label that in Huehuetenango, Guatemala, the cooked leaves of *L. procerrima* are reputed to be efficacious in treating bad eyes. *Lawrance 795* from Colombia and *Steyermark 61115* from Venezuela indicated *L. procerrima* to be a good forage plant for domestic animals. This seems likely considering the large, thick leaves. I think it is doubtful, however, that the species ever occurs in large enough populations to be used extensively for this purpose. The collection of Sinart (S. 39) reported on the label that the Carib Indians of British Honduras use this species for broom making.

BELIZE. CAYO: San Augustin, *Bartlett & Hunt 268* (US). Mi 28, Hummingbird Hwy., *Dwyer 11416* (MO). S of Belmopan, *Dwyer & Liesner 12075* (MO). San Augustin, *Lundell 6571* (F, NY, US). STANN CREEK: Toward Stann Creek, *Dwyer 11194* (MO). Stann Creek Valley, *Gentle 2638* (F, GH, NY). Carib Reserve, *Sinart 39* (US). TOLEDO: Monkey River, *Gentle 3692* (F, GH, MO, NY, US).

BRAZIL. AMAZONAS: Rio Negro, São Gabriel, *Baldwin 3538* (US). Mouth of Rio Uaupes, *Baldwin 3552* (US). Rio Negro, *Black 48-2496* (US); *Froés 21119* (NY, US); *Luetzeburg 22114* (NY). Tapuruquara, *Prance et al. 15832* (NY). RORAIMA: Serra dos Surucucus, *Prance et al. 10052* (MO).

COLOMBIA. ANTIOQUIA: 26 km S of Zaragoza, *Denslow 2373* (MO). Malena, *Gutiérrez & Barkley 17C145* (US); *Killip 34505* (US); *Pennell 3777* (NY, US). Entre Bocas y Anori, *Soejarto et al. 4346* (MO). Vic. of Medellín, *Toro 1100* (NY). BOYACA: N of Bogotá, *Lawrance 795* (GH, MO, RB, UC, US). CAUCA: El Tambo, *Idrobo & Fernández 108* (COL, US). CAQUETÁ: 53 km SE of Guadalupe, *Davidse et al. 5628A* (MO). 28 km S of Morelia, *Davidse et al. 5656* (MO). 23 km N of Florencia, *Davidse et al. 5764* (MO). 10 km N of Florencia, *Plowman & Kennedy 2246* (US). CHOCÓ: Bahía Solano, *Warner & White 34* (MO). CUNDINAMARCA: 20 km NW of Villavicencio, *Davidse & Llanos 5523* (MO). Iconozo, *Pennell 2870* (NY). HUILA: E of Neiva, *Rusby & Pennell 516* (NY). MAGDALENA: Rincón Hondo, *Allen 367* (MO). San Andres de la Sierra, *Pittier 1645* (US). Vic. of Santa Marta, *Seifriz 165* (US); *Smith 117* (F, MO, NY, US, WIS). META: Sierra de La Macarena, *Chaparro et al. 107* (MO); *García-Barriga & Jaramillo 17093A* (COL). Guamal, *Jaramillo et al. 1019* (COL). Near Villavicencio, *Killip 34505* (COL); *Niceforo s.n.* (COL). La Macarena, *Philipson et al. 1651* (COL). San Juan de Arama, *Pinto & Sastre 1105* (COL). Villavicencio, *Zuluaga 187* (COL). NORTE DE SANTANDER: Entre El Caraño y El Indio, *Cuatrecasas 13024* (COL, US). PUTUMAYO: Mocoa, *García-Barriga 4635* (COL). VALLE: Dagra Valley, *Killip 5366* (NY, US). Santa Rosa, *Killip 11564* (NY, US).

COSTA RICA. ALAJUELA: San Ramón, *Brenner 6514* (F). Nuestro Amo, *Jiménez 532* (US). CARTAGO: Near Muñeco, *Lent 1887* (F). IICA, *León 888* (US). Turrialba, *Pohl & Calderón 10356* (ISC). 18 km N of Turrialba, *Pohl & Davidse 10824* (F). GUANACASTE: Vic. of Liberia, *Daubenmire 399* (F); *Pohl & Davidse 10639* (ISC). 6 km S of La Cruz, *Pohl & Davidse 11317* (ISC). Vic. of Liberia, *Pohl & Davidse 11328* (ISC). HEREDIA: 35 km NE of Alajuela, *Taylor 4520* (MO). LIMÓN: 6 km W of Guápiles, *Pohl & Davidse 10016* (ISC). 1 km SW of Pueblo Nuevo, *Pohl & Davidse 11096* (ISC). PUNTARENAS: Puntarenas, *Hitchcock 8572* (US). Vic. of Boruca, *Pohl & Davidse 10993* (ISC). N of San Vito de Java, *Pohl & Davidse 11163* (ISC). SAN JOSÉ: San José, *Hitchcock 8445* (US). Vic. of San Isidro del General, *Molina et al. 18221* (F, NY, US); *Pittier 12057* (ISC, P, US). E of San Ignacio, *Pohl & Davidse 10526* (ISC). Río Conejo, *Pohl & Davidse 11055* (ISC). 8 km SW of Guarumal, *Pohl & Pinnette 13293* (MO). Vic. of El General, *Skutch 2167* (GH, MO, NY, US).

ECUADOR: Rd. from Napo to Puyo, *Ellenberg 3282* (MO).

EL SALVADOR. CHALATENANGO: 7 km SSE of La Palma, *Davidse & Pohl 2072* (ISC, MO). San Francisco del Túnel, *Weberling 2515* (M). MORAZÁN: Montes de Cacaguatique, *Tucker 777* (F, ISC, UC, US). SAN MIGUEL: Volcán de San Miguel, *Stevens & Stergios 149* (MO). SAN SALVADOR: San Salvador, *Calderón 849* (NY, US). Nördlich Cruzadillo, *Rohweder 1396* (MO). Vic. Ayutuxtepeque, *Standley 20512* (US). SANTA ANA: Metapán, *Cruz Guevara 51* (MO).

GUATEMALA. ALTA VERAPAZ: Cobán, *Bernoulli & Cario 968* (GOET). Near Secoyctí, *Cook & Griggs 119* (US). 4 mi to Oxec, *Croat 41575* (MO). Cubilqüitz, *von Tuerckheim 1028* (F, MO, US). Cobán, *von Tuerckheim 2486* (US). 12 km W of San Cristóbal, *Standley 89731* (F). Near Santa Cruz, *Standley 92783* (F). CHIQUIMULA: 6 km S of Quezaltepeque, *Harmon & Dwyer 3723* (MO). CHIMALTENANGO: Variedades, *Johnston 979* (F). Between Chimaltenango and San Martin Jilotepeque, *Standley 64296* (F). ESCUINTLA: Texcuaco, *Morales s.n.* (F). Near Escuintla, *Standley 63925* (F). GUATEMALA: Vic. of Guatemala, *Harmon 1822* (MO); *Hitchcock 9067* (US). 10 km S of San Raimundo, *Standley 62914* (F, US). Guatemala, *Tonduz 1850* (US). HUEHUETENANGO: 7 km SE of San Antonio Huiste, *Melhuis & Goodman 3630* (F, ISC). Around Ixcan, *Steyermark 49201* (F). IZABAL: Lago Izabal, *Blake 7836* (US). Ca. 7 mi S of Puerto Barrios, *Croat 41780* (MO). Vic. of Quiriguá, *Standley 24244* (US). Vic. of Puerto Barrios, *Standley 25045* (US). N of Quiriguá, *Weatherwax 85* (US). JALAPA: E of Jalapa, *Standley 77029* (F). Between Jalapa and San Pedro Pinula, *Standley 77036* (F). QUETZALTENANGO: Quetzaltenango, *Palmer 6247* (US). Colomba, *Skutch 1298* (F, GH, US). SAN MARCOS: Near San Rafael, *Croat 40779* (MO).

SANTA ROSA: Santa Rosa, *Heyde & Lux 3906* (US). Near Cuilapa, *Standley 77686* (F). Vic. of Platanares, *Standley 79136* (F). SOLOLÁ: Volcán Atitlán, *Steyermark 47989* (F). SUCHITEPÉQUEZ: Volcán Zunil, *Steyermark 35269* (F). ZACAPA: Sierra de las Minas, *Steyermark 29588* (F), *42250* (F).

GUYANA. Vic. of Kaieteur Falls, *Cowan & Soderstrom 1889* (NY, US). Potaro River, *Jenman 813* (US). Kaieteur Savanna, *Sandwith 1322* (NY, US); *Tutin 630* (US).

HONDURAS. ATLANTIDA: Vic. of La Ceiba, *Yuncker et al. 8594* (GH, MO, NY). COMAYAUGA: Near El Achote, *Yuncker et al. 5898* (GH, MO, US). COPÁN: 8 km de Santa Rosa de Copán, *Molina 12872* (US). EL PARAÍSO: 32 km W of Danlí, *Davidse & Pohl 2146* (ISC). Between La Vistada de San José and Fátima, *Molina 11173* (F). Güinope, *Rodríguez 1865* (F). MORAZÁN: Vic. of El Zamorano, *Davidse & Pohl 2081* (ISC, MO). Between San Juancito and Valle de Angeles, *Davidse & Pohl 2125* (ISC). 4 km N of Venta, *Davidse & Pohl 2160* (ISC). Vic. of El Zamorano, *Davidse & Pohl 2161* (ISC, MO); *Freytag 242* (WIS); *Glassman 1759* (F). Río de la Orilla, *Molina 228* (F, MO, US). Quebrada Terragra, *Molina 4074* (F). 28 km from Tegucigalpa, *Pilz & Pilz 1325* (MO). Vic. of El Zamorano, *Pohl 12504* (ISC), *12531* (ISC). San Antonio de Oriente, *Rodríguez 653* (F). Vic. of El Zamorano, *Standley 300* (F). Near Río Yeguare, *Standley & Williams 1623* (F). Vic. of El Zamorano, *Standley et al. 5087* (F), *22899* (F), *23323* (F), *24854* (F). San Antonio de Oriente, *Swallen 10911* (US), *10970* (US). Mt. Uyuca, *Swallen 11303* (US). Santa Inés, *Williams & Molina 10408* (US). Quebrada Triquilapa, *Williams & Molina 11983* (F, GH). Agua Amarilla, *Williams & Molina 12157* (F). OCOTEPEQUE: 10 km from Nueva Ocotepeque, *Molina 22206* (F). La Montañita, *Molina 22561* (F). SANTA BÁRBARA: 1 km from Santa Bárbara, *Molina 3665* (F).

MEXICO. CHIAPAS: 17 km N of Tuxtla Gutiérrez, *Breedlove 13905* (F). Near Rizo de Oro, *Breedlove & Thorne 20535* (DS, MO). N of Ocosingo, *Breedlove & Smith 22112* (DS, MO). Near Cerro Blanco, *Breedlove 24080* (DS, MO). 13 km N of Berriozábal, *Breedlove 26297* (DS, MO). 6–12 km N of Palenque, *Breedlove 26497* (DS, MO). 6–8 km N of Ocosingo, *Breedlove 27903* (DS, MO). 12 km S of Tuxtla Gutiérrez, *Breedlove 28036* (DS, MO). Lagunas de Monte Bello National Park, *Breedlove 37041* (DS). 21 km S of Tonalá, *Breedlove 38121* (DS). Vic. of Pinchucalo, *Chavelas et al. 337* (MEXU), *1647* (MEXU), *2255* (MEXU). 5 mi N of Ixtacomitán, *Davidse & Davidse 9435* (MO). Cuamúchil, *Enriquez 6777* (MEXU). Vic. of Ocuilapa, *Nelson 3055* (GH, US). 10 km S of Jitotol, *Roe et al. 1154* (WIS). Km 33 S of Sureste, *Roe et al. 1367* (WIS). Ti-Ha', *Ton 1450* (F, NY). Tenejapa, *Ton 1653* (NY). El Bosque to Simojovel, *Ton 3077* (NY). SW of Presa de Malpaso, *Ton 3294* (F). Cerro Palenque, *Matuda 3718* (F, GH, MEXU, NY, US). Between Escuipulas and Canada Honda, *Xolocotzi X-323* (US). COLIMA: Near Minatitlán, *Beetle et al. M-3528* (MO). Alzada, *Hitchcock 7085* (US). DURANGO: 1.8 mi W of La Guayanerga, *Jackson 134* (NY). GUERRERO: Galeana, *Hinton 14690* (GH, NY, US). JALISCO: Between Manzanillo and Puerto Vallarta, *Beetle et al. M-3579* (MO). 4 mi NNE of Talpa de Allende, *McVaugh 20155* (NY). 11 mi S of Talpa de Allende, *McVaugh 20243* (NY). Río Blanco, *Palmer 535* (F, GH, MEXU, MO, NY, US). Vic. of Guadalajara, *Pringle 1732* (F, GH, MO, NY, P, UC, US), *11760* (US). Sierra de Los Corales, *Rzedowski 17443* (US). 8 mi W of Guadalajara, *Soderstrom 611* (MEXU, US). Tequila, *Xolocotzi et al. X-2749* (US). MÉXICO: Temascaltepec, *Hinton 1948* (MO, NY, US), *2408* (NY, US). Tejupilco, *Matuda 27456* (MEXU). Santa Tomás, *Matuda 29360* (US). MICHOACÁN: 22 km S of Uruapan, *King & Soderstrom 4802* (NY, UC, US). El Ocote, *Langlassé 540* (GH, US). 7 mi SW of Uruapan, *Leavenworth & Leavenworth 1255* (US). Near Uruapan, *Woronow 2706* (US). NAYARIT: Jalisco, *Ferris 5847* (GH, US). 10 mi E of Jalcocatlán, *McVaugh 13357* (MEXU, US). 2 mi W of Mazatán, *McVaugh 19101* (NY). Tepic to Santiago, *Mexia 628* (F, MO, NY, UC, US). 1 km N of El Cuatante, *Rzedowski 17844* (US). OAXACA: N of Matías Romero, *Beetle M-3096* (MO). 18 mi W of jct. Mex. 147 and 185, *Brunken & Perino 292* (MO). 151 km SW of Oaxaca, *Brunken & Perino 371* (MO). Tuxtepec to Pueblo Viejo, *Chavelas & Pérez 6* (MEXU). Chiltepec, *Martínez-Calderón 239* (GH, UC, US). 21 km S of Valle Nacional, *Mickel 1463* (NY). 12 km S of Valle Nacional, *Mickel 1485* (NY). 35 km S of Juchatengo, *Roe et al. 586* (WIS). Tuxtepec, *Sousa 1559* (MEXU). 3 km E de Sarabia, *Vasquez 1443* (MO). PUEBLA: Pahuatlan to Huachinango, *Miranda 3697* (MEXU). Villa Juárez, *Sarukhán et al. 1335* (MEXU). SINALOA: Vic. of Culiacán, *Brandegee s.n.* (GH, UC). Cerro Colorado, *Gentry 5126* (GH, MO, NY, UC, US). 16 mi NE of Concordia, *Gould 12250* (UC, US). 56 km from Temascal, *Moore et al. 5697* (GH, UC, US). San Ignacio, *Ortega 169* (MEXU). 47 mi E of Villa Union, *Reeder & Reeder 2446* (GH). Near Colomas, *Rose 1687* (US). TABASCO: Huiman-

guillo, *Barlow 30-152* (WIS), *30-152B* (MEXU); *Discoreas 11507* (MEXU). VERACRUZ: Córdoba, *Bourgeau 1889* (P). Near Orizaba, *Bourgeau 2971* (GH, P). Zapoapan de Cabañas, *Bravo 247* (MEXU). Near Sayula, *González & Garza 8039* (MEXU). Córdoba, *Hitchcock A.G.N.H.596* (F, GH, MO, NY, P, UC, US). Orizaba, *Hitchcock 6385* (RB, US). Huitamalco, *Liebman 308* (MO). 1 mi W of Fortin, *Paxson et al. 17M671* (MEXU). Vic. of San José de Mata Clara, *Pohl & Davidse 11812* (ISC). Zaruapan, *Purpus 7813* (GH, MO, NY, US). Near Teocello, *Soderstrom 469* (US).

NICARAGUA. CARAZO: Jinotepe, *Hitchcock 8694* (US). MANAGUA: Vic. of Casa Colorado, *Standley 8775* (F). ZELAYA: W of Bluefields, *Atwood 4182* (MO). Río Lecus, *Davidse & Pohl 2347* (ISC, MO). Near Waspam, *Molina 14904* (F, NY). Río Lecus, *Pohl & Erickson 12701* (ISC), *12702* (MO).

PANAMA. BOCAS DEL TORO: Water Valley, *von Wedel 759* (GH, MO, US). Vic. of Chiriquí Lagoon, *von Wedel 1186* (GH, MO, US). CANAL ZONE: Barro Colorado Island, *Aviles 111* (F, MO); *Croat 6108* (NY), *6379* (MO). Fort Sherman, *Duke 4346* (MO). Military Rd. K-9, *Ebinger 526* (MO, US). Frijoles, *Foster & Kennedy 2026* (MO). Pipeline Rd., *Gentry 1930* (MO). Miraflores Lake, *Harvey 5135* (F). Between Pedro Miguel and Corozal, *Hitchcock 7961* (US). Gatún, *Hitchcock 7984* (US). Between Frijoles and Bohío, *Hitchcock 8393* (GH, UC, US). Ancón, *Killip 4024* (US), *12066* (US). 15–20 mi NW of Gamboa, *Mori & Kallunki 1731* (MO). 0.5 km S of Summit Gardens, *Nee 7386* (MO). 9 km NW of Gamboa, *Nee 7656* (MO). 1 km N of Gamboa, *Nee 7766* (MO). Empire to Mandinga, *Piper 5280* (US). Between Corozal and Ancón, *Pittier 6774* (US). Balboa, *Rowlee & Stork 945* (NY, US); *Standley 26055* (MO, US). Vic. of Summit, *Standley 30100* (US). Near Miraflores Lake, *Tyson 1378* (MO). Fort Sherman, *Tyson & Chu 1689* (MO). 12 mi N of Gamboa, *Tyson 6656* (MO). Near Fort Lorenzo, *Witherspoon & Witherspoon 8790* (MO). CHIRIQUÍ: NE of Fortuna, *Correa et al. 2262* (MO). Near San Felix, *Croat 33410* (MO). Llanos Francia, *Dwyer & Lallathin 8724* (MO). W of Fortuna, *Folsom et al. 5359* (MO). Vic. of Boquete, *Hitchcock 8283* (US). 4.1 mi from Boquete, *Kirkbride 90* (MO, NY). 17 km NE of San Felix, *Nee 10684* (MO). COCLÉ: El Valle, *Dwyer 1820* (MO). 7 km N of El Cope, *Folsom & Collins 6431* (MO). From El Valle to La Mesa, *Spellman et al. 559* (MO). COLÓN: Maria Chiquita, *Dwyer & Kirkbride 7800* (MO). DARIÉN: Vic. of Caná, *Croat 37633* (MO); *Sullivan 634* (MO). PANAMÁ: Cerro Campana, *Bartlett & Lasser 16902* (MO). Rd. to Cerro Campana, *Croat 12037* (MO). Panamá Viejo, *Duke 5722A* (MO). Cerro Campana, *Duke 5959* (GH, MO). Cerro Azul, *Dwyer 2635* (MO). Cerro Jefe, *Dwyer et al. 3512* (MO). San José Island, *Erlanson 383* (GH, NY, US); *Johnston 296* (GH), *442* (GH, US). Altos del Río Pacora, *Lewis et al. 2301* (COL, MO, UC). Cerro Campana, *Nee 6870* (MO). El Llano-Cartí Rd., *Nee 7878* (MO). Mouth of Río Chagres, *Piper 5948* (US). Vic. of Arenoso, *Seibert 628* (GH, MO, NY, US). Taboga Island, *Standley 27055* (US). Cerro Azul, *Tyson 2103* (MO). Cerro Campana, *Tyson et al. 2340* (MO). Sabago Island, *Tyson & Loftin 5112* (MO). Near Arraiján, *Woodson et al. 1399* (GH, MO, NY, US). Isla Taboga, *Woodson et al. 1453* (GH, MO, NY, US). SAN BLAS: SE of Puerto Obaldia, *Croat 16704* (MO).

PERU. SAN MARTIN: Tarapote, *Williams 6081* (F, GH, US). Alto Río Huallago, *Williams 6611* (F, US).

VENEZUELA. AMAZONAS: Sierra Parima, *Steyermark 105995* (MO). ANZOÁTEGUI: Cerro La Danta, *Steyermark 61115* (F, US, VEN). ARAGUA: Via Cumbre de Choroní, *Benítez de Rojas 395* (MO, MY). Rancho Grande, *Chase 12464* (US); *Davidse 3022* (ISC, MO). Alto de Caroní, *Lasser 1534* (NY, US). Maracay–Choroní, *Montaldo & Ramia 3262* (MO). Rancho Grande, *Motaldo 3581* (MY). Güigüe, *Müller 759* (VEN). Between Maracay and Ocumare, *Pittier 11854* (NY, US, VEN). Valley of Choroní, *Pittier 13918* (F, US, VEN). Rancho Grande, *Tamayo s.n.* (VEN). Maracay–Choroní, *Trujillo 5038* (MY), *10561* (MY). BARINAS: 43 km NW of Barinas, *Davidse 3193* (ISC, MO). BOLÍVAR: La Gran Sabana, *Davidse et al. 4783* (MO). Cerro Bolívar, *Maguire 32663* (NY, US, VEN). Cabeceras de Río Chicanán, *Steyermark 89542* (F, NY, US, VEN). Santa Elena, *Tamayo 2720* (US, VEN). CARABOBO: Valle de Chiragua, *Barrus s.n.* (VEN). DISTRITO FEDERAL: Caoma, *Jahn 14* (GH, US), *314* (US). El Limón, *Pittier 8059* (GH, US). MÉRIDA: Santo Domingo, *Bernardi 993* (VEN). Near Palomitas, *Box 3770* (MY). MIRANDA: Vic. of Sebastopal, *Badillo 311* (VEN). 34 km NW of Santa Lucia, *Davidse 2910* (ISC, MO). Between Los Canales and El Encante, *Lasser 675* (VEN). Between San Antonio and Los Altos, *Tamayo 1509* (VEN). Los Teques, *Williams 12424* (F). TRUJILLO: 37 km from Trujillo, *Breteler 4128* (MO, US).

10. **Lasiacis rhizophora** (Fourn.) Hitchc., Proc. Biol. Soc. Wash. 24: 145. 1911

Panicum rhizophorum Forun., Mex. Pl. 2: 31. 1886. TYPE: Mexico, region d'Orizaba, 10 Sep. 1866, *Bourgeau 3025* (P, lectotype; F, GH, MO in part, US, isolectotypes).

Perennial; culms creeping, slender, rooting at the lower nodes, freely branching and forming tangled colonies, the upper parts of the culms erect to 1 m, especially when producing inflorescences but gradually reclining with further growth; internodes 2–3 mm thick, solid, herbaceous, puberulent, especially toward the apex, sometimes restricted to the apex; nodes glabrous or puberulent; sheaths usually shorter than the internodes, usually puberulent, less often hirsute or hispid with papillose hairs to 2.0 mm long, rarely glabrous, the overlapping sheath margin usually densely ciliate at the apex, the auricular hairs at the sheath apex often prominent, 1.0–4.0 mm long; collar glabrous and usually ciliate on one margin, rarely puberulent; ligule membranous, 0.4–0.7(–1.1) mm long, prominently ciliate with hairs 1.5–3.5 mm long, glabrous on the back; blades 8–13(–17) cm long, 1.6–3.7 cm wide, elliptic-lanceolate, lanceolate, or narrowly lanceolate, the upper surface sparsely to moderately hispid or hispidulous with hairs to 1.5 mm long, scabrid, occasionally glabrous, the lower surface usually puberulent, occasionally hispidulous, hispid, or glabrous, the apex acuminate, the base strongly asymmetrical, the larger lobe slightly cordate and clasping the culm; panicles 10–19(–24) cm long, the longest branch 3–11 cm long, the branches ascending or spreading, scabrous, or puberulent, bearing spikelets markedly clustered in pairs or small groups toward the tips of the branches, the lower portions of the branches often naked, the pulvini usually puberulent, the lower ones occasionally pubescent, the pedicels scabrid or pubescent; spikelets (3.1–)3.3–3.9(–4.0) mm long; first glume 1.4–2.1 mm long, 5–7-nerved; second glume 7–9-nerved; sterile floret without a flower, or rarely with rudimentary staminate flowers, the lemma 7–9-nerved, the palea ¾ or less the length of the fertile floret; fertile floret 2.9–3.2 mm long, 1.7–2.2 mm wide, black to dark brown, the anthers 1.6–1.9 mm long, white, the stigmas purple; caryopsis 2.2–2.4 mm long, 1.7–1.9 mm wide; chromosome number $n = 18$.

Ecology: *Lasiacis rhizophora* is primarily a montane forest species having been collected at elevations from 600 to 2,000 m. It may inhabit undisturbed oak and cloud forests, but it is more commonly collected along forest margins and trails, along streams, and even in more highly disturbed areas such as coffee plantations. Spikelet-bearing plants have been collected from July through February.

Distribution: Specimens have been collected from Guerrero, Morelos, Puebla, and Veracruz in Mexico south to Colombia. Noticeably absent are collections from the Yucatán Peninsula, including Belize, and El Salvador.

Hitchcock (1913, 1920) selected the lectotype. The isolectotype at MO actually represents a mixture of two plants, one a sterile shoot of *L. rhizophora* with solid culms and roots at the nodes, the other a fertile shoot of *L. ruscifolia* that has hollow culms and a compacted inflorescence with evenly distributed

spikelets. One of the syntypes cited by Fournier (1886) in the original description is *Belanger 390* from Martinique in the West Indies. This is not *L. rhizophora* but rather *L. sorghoidea*. *Lasiacis rhizophora* is strictly continental and is not known from any of the West Indian islands. The Belanger specimen from the Paris Herbarium has a label stating it be a type, however, there does not appear to be any published reference citing this specimen as the type of *P. rhizophorum*.

Considerable doubt has existed considering the effective date of publication for Fournier's grass species included in *Mexicanas Plantas*. Reeder & Reeder (1974) have reviewed this problem, and I have followed their recommendation in using 1886 as the effective date of publication.

Lasiacis rhizophora is a well-marked species characterized by its procumbent growth habit, solid culms rooting at the nodes, broad blades, and inflorescences whose branches are naked below and bear spikelets in pairs or small clusters toward the tips of the branches. This species is confused most easily with *L. ruscifolia*, especially if the lower root producing nodes are missing. The two species can, however, be very readily distinguished since *L. ruscifolia* has hollow culms; furthermore, *L. ruscifolia* has inflorescences with evenly distributed, larger spikelets.

Pittier et al. (1945) credited *L. rhizophora* to Venezuela. This was an error since the specimens upon which the report is based (*Pittier 14162*, US, VEN) is a depauperate specimen of *L. anomala* in which the culms have bent down and secondarily rooted at the nodes. As noted under *L. grisebachii* var. *lindelieana*, Hitchcock (1936) wrongly credited *L. rhizophora* to Cuba. The report of *L. rhizophora* for the Dominican Republic was based on *Ekman 13200*, a sterile specimen. Although this specimen does have the solid culms and ciliate ligules characteristic of *L. rhizophora*, it is quite different in its roots and branching pattern. It does not seem to be *L. rhizophora*, and even its inclusion in *Lasiacis* is uncertain.

Common names: Colombia: Magdalena, arrocito, *Cuatrecasas & Cuatrecasas* 25383.

COLOMBIA. MAGDALENA: Sierra de Perijá, *Cuatrecasas & Romero-Castañeda* 25383 (COL, US). VALLE: La Cumbra, *Killip 11607* (NY, US).

COSTA RICA. ALAJUELA: Near Grecia, *Anderson 1375* (US). La Palma de San Ramón, *Brenes 5371* (F, US). San Miguel de San Ramón, *Brenes 20300* (F, NY). Maravilla, *Jiménez 168* (US), *703* (US). Zarcero, *Smith H41* (MO), *A595* (MO), *48-200* (US). CARTAGO: Near San Ramón, *Brenes 4560* (F, US). Navarro, *Solís 5807* (F). 4 km SW of Tejar, *Taylor 4577* (MO). GUANACASTE: Vic. of Tilarán, *Standley & Valerio 44236* (US), *45498* (US). PUNTARENAS: Monteverde, *Jiménez 1271* (F, NY). Cañas Gordas, *Pittier 11015* (US). SAN JOSÉ: Vic. of San José, *Hitchcock 8502* (US); *Jiménez s.n.* (US). 1 mi N of San Gabriel, *Pohl & Davidse 11179* (ISC). S of San Antonio, *Pohl & Davidse 11481* (ISC). S of Curridabat, *Pohl & Davidse 11694* (ISC). Vic. of Santa Maria de Dota, *Standley 42531* (US); *Standley & Valerio 43264* (US), *44071* (US).

GUATEMALA. ALTA VERAPAZ: 10 km of Cobán, *Harmon & Dwyer 4280* (MO). Cobán, *von Tuerckheim 715* (F, GH, MO, P, US). CHIQUIMULA: 3 mi N of Jocatán, *Steyermark 31581* (F). GUATEMALA: 7 mi E of Guatemala, *Harmon 2932* (MO). Guatemala, *Hitchcock 9051* (UC, US). Between San Lucas and Guatemala, *Molina 21091* (GH, NY). Vic. of San Andrecillo, *Molina & Molina 27554* (MO). Guatemala, *Morales 1105* (F). Barranca de las Vacas, *Standley 59532* (F). HUEHUETENANGO: Crossing of Río San Juan Ixtán, *Standley 82944* (F). Between Ixcán and Finca San Rafael, *Steyermark 49468* (F). JALAPA: Cerro Alcoba, *Steyermark 32539* (F). QUETZALTENANGO: Between Finca Pirineos and Patzulín, *Standley 86730* (F, US), *86758* (F), *87059* (F). RETALHULEU: Retalhuleu, *de Koninck 238*

(US). SACATÈPÉQUEZ: Ca. 20 km W of Guatemala City, *Davidson 3288* (MO). Cuesta de las Cañas, *Molina 15446* (US). SAN MARCOS: Near Aldea Fraternidad, *Williams et al. 26039* (F, GH, ISC, NY, US, WIS). SANTA ROSA: Chupadero, *Heyde & Lux 3915* (GH, US). SUCHITEPÉQUEZ: Volcán Zunil, *Steyermark 35340* (F).

HONDURAS. EL PARAÍSO: El Volcán de Monsserat, *Molina 26149* (MO). 6 km SE of San Lucas, *Pohl & Davidse 12159* (ISC, MO). 8 km W of Yuscarán, *Pohl & Erickson 12748* (ISC, MO). Güinope, *Valerio 1762* (F). MORAZÁN: Cerro Uyuca, *Davidse & Pohl 2107* (ISC); *Molina 1433* (F, US). Río Yeguare, *Molina 2766* (F, GH, MO, US). Río Rancho Quemado, *Molina 18651* (F, GH, NY). Between La Vuelta del Zope and San Juan del Rancho, *Molina & Molina 25824* (MO). Cerro Uyuca, *Standley 14073* (F), *23109A* (F, US); *Swallen 10903* (US); *Williams 16851* (F, GH). 20 km N of Siguatepeque, *Williams & Williams 18422* (US).

MEXICO. CHIAPAS: 18–20 km N of Ocozocoautla, *Breedlove & Thorne 21025* (DS, MO). 42 km NE of La Trinitaria, *Breedlove & Thorne 21101* (DS, MO). 16 km NW of Rizo de Oro, *Breedlove & Smith 21703* (DS, MO). 6–8 km N of Ocosingo, *Breedlove & Smith 22173* (DS, MO). SE of Cerro Baul, *Breedlove 27602* (DS, MO). 6–8 km N of Ocosingo, *Breedlove 27923* (DS, MO). 30 km NW of Ocozocoautla, *Breedlove 28904* (DS, MO). 20 km S of Ocozocoautla, *Breedlove 29085* (DS, MO). 3 km E of Francisco Madero, *Breedlove 38025* (DS, MO). Between Escuipulas and Canada Honda, *Hernández-X. X-309* (US). Monte Cristo Salina, *Matuda 1939* (F, GH, MEXU, NY, UC, US). Sierra Madre, *Tateoka 1030* (US). GUERRERO: Galeana, *Hinton 10809* (GH, NY, US), *14633* (GH, NY, US). MORELOS: Sierra de Ocuila, *Lyonnet 2888* (US). OAXACA: *Reko 3486A* (US). VERACRUZ: Vic. of Orizaba, *Botteri 633* (GH); *Bourgeau 3025* (F, GH, P). Córdoba, *Hitchcock A.G.N.H.413* (F, GH, MO, NY, P, UC, US). Vic. of Orizaba, *Muller 2029* (NY); *Seaton 60* (F, GH, US).

NICARAGUA. GRANADA: Mt. Mombacho, *Grant 821* (GH, US). JINOTEGA: 3.8 mi SE of Yalí, *Croat 42914* (MO). 5–8 mi SW of Jinotega, *Croat 43046* (MO). Near Santa Maria de Ostuma, *Hawkes et al. 2192* (F).

PANAMA. CHIRIQUÍ: Volcán Chiriquí, *Davidse & D'Arcy 10158* (MO).

11a. **Lasiacis rugelii** (Griseb.) Hitchc. var. **rugelii**, Bot. Gaz. (Crawfordsville) 51: 302. 1911.

Panicum rugelii Griseb., Cat. Pl. Cub. 233. 1866. TYPE: Cuba, in montibus Mantanzas, scandens in fruticibus, 1849, *Rugel 188* (GOET, lectotype; GH, isolectotype).

Lasiacis papillosa Swallen, Publ. Carnegie Inst. Wash. 436. 349. 1934. TYPE: Mexico, Yucatán, Peto, erect in bush, 26–27 July 1932, *Swallen 2707* (US, holotype; MO, isotype).

L. lancifolia Swallen, Publ. Carnegie Inst. Wash. 436: 349. 1934. TYPE: Mexico, Yucatán, Muna, along trail in hills, culms erect, 22–23 July 1932, *Swallen 2664* (US-1537246, holotype; GH, US, 4 sheets, isotypes).

Perennial; culms erect or clambering and climbing, 0.6–3 mm long, in clumps, the upper parts of young culms often strongly zigzag, the older culms highly branched, often with fascicles of secondary branches on the primary culm; internodes hollow, 2–5 mm thick, lignified, usually papillose-puberulent with hairs often appressed, becoming glabrous in age but roughened due to remaining papillae, rarely glabrous except for a line of puberulence, completely glabrous, or densely short pubescent with hairs to 0.7 mm long; nodes usually glabrous, occasionally sparsely to densely puberulent; sheaths spreading puberulent, often densely puberulent or velutinous, the upper margin ciliate with hairs 0.5–2.0 mm long, occasionally the lower margin ciliate on the upper half, the auricular hairs 1–2 mm long; collar usually puberulent, sometimes with an additional line of dense pubescence at its base with hairs to 1.0 mm long; ligule very inconspicuous, 0.1–0.3 mm long, glabrous, or ciliolate with hairs to 0.5 mm long; blades lanceolate to ovate-lanceolate, (2.5–)3.5–5.5(–9.5) cm long, (0.5–)0.8–1.5 (–2.2) cm wide, the upper surface sparsely to densely puberulent, rarely glabrous, the lower surface puberulent or velutinous, rarely glabrous, the apex acute

to acuminate, the base asymmetrical, the margin scabrid; panicles small, 2–10(–14) cm long, the longest branch 1–5.5 cm long, the branches bearing few, evenly distributed spikelets, the lower branches and most branchlets reflexed or at least widely spreading, the branches puberulent, often densely so toward the base, the upper part of the panicle occasionally only scabrid, the pulvini puberulent; spikelets obovate, (3.8–)4.0–4.8 mm long; first glume 1.5–2.1 mm long; 7–9-nerved; second glume 9–11-nerved; sterile floret without a flower, the sterile palea ¾ to equal the length of the fertile floret, the lemma 9–11-nerved; fertile floret 3.8–4.1 mm long, 2.3–2.6 mm wide, light tan at maturity; caryopsis 2.4–2.6 mm long, 1.9–2.1 mm wide, whitish.

Ecology: *Lasiacis rugelii* var. *rugelii* is an inhabitant of wooded areas and is most commonly collected in thickets, along trails, forest margins, and in secondary forests, as well as in pine forests in Cuba. The only elevation records give 100 and 700 m. Plants bearing spikelets have been collected in all months except May, but the main flowering period extends from July to March.

Distribution: *Lasiacis rugelii* is found in Cuba, Hispaniola (infrequently), San Luis Potosí, Veracruz, and the Yucatán Peninsula, including Belize and parts of Guatemala and Mexico.

Grisebach (1866) cited two syntypes (*Rugel 188* and *Wright 3465*) with his description of *Panicum rugelii*. Hitchcock (1909) chose *Rugel 188* as the lectotype.

This species is characterized by its erect, usually puberulent culms, small broad blades, and sparsely flowered inflorescences with reflexed or widely spreading branches bearing obovate spikelets. It is closely related to *L. divaricata* var. *divaricata*. It can be distinguished from this taxon by its shorter and wider blades and usually puberulent culms and leaves.

Hitchcock (1936) described *L. rugelii* as prostrate. He may have based this description largely on a specimen (*Hitchcock 176*) he collected in Cuba. The label with the specimens notes, "creeping, not climbing as *P. divaricatum*." However, *L. rugelii* is primarily an erect species with culms climbing into shrubby vegetation. All Cuban specimens which show culm bases are clearly erect plants. An Ekman specimen (*Ekman 795*) bears a label stating that "this species has a tolerably strong central cane up to 2 m high." Even in the original description, Grisebach (1866) described this species as scandent, basing this description on Rugel's observation. It is possible that Hitchcock collected a specimen which had secondarily become procumbent. This happens occasionally when young, thin stems which are not supported become lodged and root at the nodes. Having recognized the essentially erect growth habit of *L. rugelii*, it then becomes necessary to reduce *L. papillosa* Swallen to synonymy since the distinction between these two species was based almost entirely on this character. This is evident from the differential diagnosis Swallen (1934) provided following the original description of *L. papillosa*: "Similar to *Lasiacis rugelii* (Griseb.) Hitchc., but that species is strictly prostrate." The West Indian and Central American populations are very similar in other characters besides culm morphology, although the Central American plants tend to be somewhat more robust.

Only two collections of *L. rugelii* from Hispaniola were seen; these have culm internodes that are glabrous except for a line of pubescence extending down from the sheath margin.

When describing *L. lancifolia*, Swallen (1934) stated in the differential diagnosis that this species was related to *L. ruscifolia*. I disagree with Swallen. The type specimen is identical to numerous Yucatán collections of *L. rugelii* in the shape and pubescence of the leaves and the size and type of inflorescence and spikelets. The type does differ from all Central American specimens of this species in its completely glabrous culm. I believe this lack of culm pubescence does not indicate specific rank. It seems to be a further step in the reduction of culm pubescence already noted in the Hispaniolan representatives of this species. The type collection, which is excellently documented with four sheets showing different segments of mature and immature culms, is remarkable in that it represents the most vigorous plant of *L. rugelii* that I have seen. The internodes of the main culm are 9 mm thick and also bear the largest blades recorded for this species.

BELIZE. BELIZE: Western Hwy. km 35, *Croat 24770* (MO). Mi 50 New River Toll Bridge, *Dwyer 12757* (MO). Maskall, *Gentle 1218* (GH, MO, NY, US). Belize-Cayo Rd., *Gentle 9605* (US). CAYO: Macal River, *Dwyer & Liesner 12284* (MO). 39 mi sect. of Hummingbird Hwy., *Gentle 8974* (F, IJ, NY, UC, US). Belize-Cayo Rd., *Gentle 9605* (US), *9691* (IJ, UC, US); *Rose Innes 49* (IJ, ISC). San Augustin, *Lundell 6840* (F, GH, MO, NY, US). 8 mi SW of El Cayo, *Proctor 29550* (IJ). Millionario, *Proctor 29865* (IJ). COROZAL: Corozal, *Gentle 560* (US). ORANGE WALK: S of Orange Walk, *Croat 24990* (MO). Honey Camp, *Lundell 91* (F, US), *550* (MO, US); *Meyer 56* (F). STANN CREEK: Commerce Bight Pine Ridge, *Gentle 8064* (F, GH, US). Stann Creek to Siltee Rd., *Lundell 6840* (US), *7943* (US). TOLEDO: Monkey River, *Gentle 4249* (MO).

CUBA. HABANA: Marianao, *Ekman A.G.N.H.795* (F, GH, MO, NY, P). Lomas de Camoa, *Ekman 13516* (US). San Antonio, *Hitchcock 176* (ISC, US). La Vigia Tapaste, *León 10668* (GH). San Miguel de Casanova, *León 12458* (US), *12459* (US), *12460* (US). ISLA DE PINOS: Coe's Camp, *Britton & Wilson 14860* (F, GH, NY). Cayo del Res, *Ekman 12446* (NY, US). MANTANZAS: Vic. of Mantanzas, *Britton et al. 106* (NY); *Ekman 16489* (US). Boca de Canasí, *León 13698* (US). ORIENTE: Guatánamo, *Ekman 10306* (F, US). Sierra de Nigre, *Ekman 15242* (US). Peninsula de Cabo Cruz, *Ekman 16151* (F, NY, US). Cobra Range, *León et al. 10608* (GH). PINAR DEL RÍO: Near Taco-Taco, *Barber 3790* (F, NY). Rosario Mts., *León 15103* (GH). Sierra de Anafe, *Wilson 11449* (F, NY, US).

DOMINICAN REPUBLIC. PUERTO PLATA: Sosúa, *Ekman 14531* (US).

GUATEMALA. ALTA VERAPAZ: 15 mi W of Telemán, *Croat 41538* (MO). Below Tamahú, *Standley 91779* (F, US). IZABAL: Above Eximbal, *Harmon & Dwyer 4334* (MO). 1 km W of Río Blanco, *Harmon & Fuentes 4883* (MO). PETÉN: Tikal Park, *Contreras 268* (F, IJ, US), *274* (US). Dos Lagunas, *Contreras 1519* (IJ, US), *1737* (IJ, US), *1738* (US). Santo Toribio, *Contreras 2692* (US). Tikal Park, *Contreras 3723* (US), *3724* (US), *3884* (US). 2 mi S of Tikal Nat. Park, *Croat 24709* (MO). Tikal Park, *Lundell 15531* (US), *15713* (US), *16106* (IJ, US), *17145* (US). 20 km E of Santa Ana, *Molina 15680* (US).

HAITI. NORD OUEST: Ile de Tortue, *Ekman 4254* (GH, IJ, US).

HONDURAS. COPÁN: 1 mi W of Copán Ruins, *Molina 30846* (MO).

MEXICO. CAMPECHE: Tuxpeña, *Lundell 918* (F, GH, NY, US), *1354* (F, GH, MO, NY, US). CHIAPAS: 32 km NW of Ocozocoautla, *Breedlove 27517* (MO). QUINTANA ROO: Lake Chichancanab, *Gaumer 23685* (F, GH, US); *Swallen 2761* (MEXU, MO, US). Tancah, *Swallen 2824* (US). Gozumel Island, *Swallen 2902* (US). SAN LUIS POTOSÍ: S of Vallejo, *Clark 6852* (MO). San Dieguito, *Palmer 151* (GH, NY, US). Río de las Gallinas, *Purpus 5438* (F, GH, MO, NY, UC, US). TABASCO: 4 km del Naranjito, *Menendez et al. 260* (MO). Balancán, *Novelo et al. 30* (MO). YUCATÁN: Chichen Itzá, *Beetle M-3793* (MO). Chichen Itzá, *Swallen 2429* (US), *2451* (US), *2464* (US). Tizimín, *Swallen 2518* (US). Uxmal, *Swallen 2640* (GH, US). Muna, *Swallen 2665* (US). Peto, *Swallen 2677* (MO, US), *2695* (US), *2696* (US), *2697* (US), *2698* (US), *2707* (US), *2712* (MO, US), *2713* (US),

2716 (US). VERACRUZ: 3 km de El Raudal, *Gómez-Pompa 84* (MEXU). Laguna Tamiahua, *Le Sueur 704* (GH, US).

11b. **Lasiacis rugelii** (Griseb.) Hitchc. var. **pohlii** Davidse, Ann. Missouri Bot. Gard. 64: 375. 1978. TYPE: Costa Rica, Cartago, 1 km NE of Pejibaye, along Río Pejibaye, growing at base of tree, ca. 700 m, 2 Nov. 1968, *Pohl & Davidse 11478* (ISC, holotype; CR, EAP, K, MO, US, isotypes).

Perennial; culms caespitose, 1–5 m long, erect at the base, rather weak, arching and climbing into vegetation, occasionally secondarily procumbent and rooting at the nodes; internodes hollow, 3–6 mm thick, usually glabrous or with a line of puberulence on one side, rarely puberulent throughout; nodes glabrous; sheaths densely puberulent, the overlapping margin ciliate with hairs 1.0 mm long, the auricular hairs 1.5 mm long; collar with a dense line of hairs at its base, the hairs to 1.0 mm long, the collar extended as a distinct pseudopetiole, 1–3 mm long; ligule an inconspicuous whitish membrane 0.1–0.4 mm long, glabrous; blades ovate-lanceolate to lanceolate, 4–7 cm long, 0.8–1.5 mm wide, the upper surface glabrous or more commonly minutely puberulent along the lower half of the midrib, the lower surface glabrous or minutely puberulent, the base asymmetrical, abruptly narrowed to nearly truncate, the margin scabrid, the apex acuminate; panicles usually not fully exserted, 3–7 cm long, the longest branch 2.0–3.5 cm long, the branches ascending to spreading, short pubescent or only scabrid, the pulvini usually puberulent, especially below; spikelets globose, 3.6–4.2 mm long; first glume 1.7–2.1(–2.5) mm long, 7–9-nerved; second glume 9-nerved; sterile floret without a flower, the lemma 9-nerved, the palea ½ to subequal the length of the fertile floret; fertile floret 3.8–4.0 mm long, 2.4–2.6 mm wide, brown; caryopsis 2.2–2.4 mm long, 2.0–2.1 mm wide.

Ecology: This variety has been collected only along margins of cloud forests or rain forests at elevations from 0 to 800 m. Collections have been made from July through January.

Distribution: Known only in Central America from Guatemala, Nicaragua, Costa Rica, and Panama.

Lasiacis rugelii var. *pohlii* is named after my major professor, a leading American agrostologist, Dr. Richard W. Pohl, Iowa State University.

It is similar in aspect to var. *rugelii* but differs in having glabrous culms (only rarely puberulent) that are not conspicuously zigzag, glabrous upper blade surfaces, a more pronounced pseudopetiole with abruptly narrowed blade base, smaller inflorescences with smaller, globose spikelets, and branches not reflexed or widely spreading.

This variety is morphologically very distinct and easily recognizable. It completely replaces var. *rugelii* in southeastern Central America. Specimens have previously been named *L. divaricata* or *L. sorghoidea* (sensu Hitchcock) apparently depending whether emphasis was placed on the puberulent sheaths or glabrous blades.

Small-leaved specimens of *L. ruscifolia* approach var. *pohlii* in appearance but can be easily recognized by their more ovate blades with broader, culm-

clasping, ciliate bases. The spikelets are quite similar to those of *L. ruscifolia* because they are globose as in the species. The fertile floret also has a rather well-developed shelf at the base of the fertile palea and lemma as in *L. ruscifolia*. It is possible that var. *pohlii* forms a link between *L. ruscifolia* and *L. rugelii*.

COSTA RICA. ALAJUELA: 3 km W of La Palma, *Pohl & Davidse 11264* (ISC). CARTAGO: Near Turrialba, *Lent 616* (F); *Pohl & Davidse 10829* (ISC). Vic. of Pejivalle, *Skutch 4655* (F, GH, MO, US). Tuis, *Tonduz 11397* (M, US). PUNTARENAS: Boruca, *León 1063* (US). SAN JOSÉ: Vic. of El General, *Skutch 3862* (GH, MO, NY, US), *4040* (GH, MO, NY, US).

GUATEMALA. ALTA VERAPAZ: Cubilqüitz, *von Tuerckheim 1481* (F, MO, US), *8620* (GH, M, UY, US).

NICARAGUA. ZELAYA: 3 km S of Bilwaskarma, *Davidse & Pohl 2303* (ISC). Río Alemán, near Esquipulas and Alemán, *Shank & Molina 4755* (F, US).

PANAMA. BOCAS DEL TORO: Almirante, N of Dos Milla, *McDaniel 5121* (MO). COCLÉ: Above El Valle de Antón, *Croat 25353* (MO), *37418* (MO); *D'Arcy & D'Arcy 6748* (MO); *Dwyer & Correa 7974* (COL, MO), *7978* (MO, UC). 7.2 km from El Valle, *Folsom 6932* (ISC, MO). Antón, La Mesa, *Kennedy et al. 2103* (MO); *Nee & Hale 9616* (MO). El Valle, *Soderstrom 2012* (MO). 5 mi N of El Valle, *Tyson et al. 2422* (NY). La Mesa, *Weaver & Foster 1657* (MO). PANAMÁ: Cerro Campana, *Croat 12142* (ISC, MO, NY), *14221* (MO). Cerro Azul, *Croat 17287* (MO). Cerro Jefe, *Davidse & D'Arcy 10103* (MO). 2 mi S of Goofy Lake, *Lewis et al. 244* (MO).

12a. **Lasiacis ruscifolia** (H.B.K.) Hitchc. var. **ruscifolia**, Proc. Biol. Soc. Wash. 24: 145. 1911.

Panicum ruscifolium H.B.K., Nov. Gen. Sp. Pl. 1: 101. 1816. TYPE: Mexico, Volcán de Jorullo, 490 hexap. (P, holotype; P, isotype).

P. compactum Schwartz, Adnot. Bot. 14. 1829, non *P. compactum* Kit., 1814. TYPE: Jamaica, *Swartz s.n.* (S, holotype, photograph S).

P. liebmannianum Fourn., Mex. Pl. 2: 33. 1886. TYPE: Mexico, Consoquitla, Aug. 1841, *Liebmann 299* (C, holotype, photograph US, fragment US; C, isotype).

P. liebmannianum var. *depauperatum* Fourn., Mex. Pl. 2: 33. 1886. TYPE: Mexico, inter Guatulco et S. Miguel del Puerto, Oct. 1842, *Liebmann 280* (C, lectotype).

Lasiacis compacta (Swartz) Hitchc., Proc. Biol. Soc. Wash. 24: 145. 1911.

L. liebmanniana (Fourn.) Hitchc., Proc. Biol. Soc. Wash. 24: 145. 1911.

L. globosa Hitchc., Contr. U.S. Natl. Herb. 17: 251. 1913. TYPE: Mexico, Acapulco and vicinity, Oct. 1894–March 1895, *Palmer 114* (US-691226, holotype; GH, MO, US-744073, isotypes).

L. glabra Swallen, Ceiba 4: 287. 1955. TYPE: Honduras, El Paraíso, road to Danlí, moist shady banks near Río San Francisco, 1 Nov. 1951, *Swallen 11193* (US-2076931, US-2153497, US-2153498, holotype; ISC, isotype).

Perennial; culms caespitose, 1–8 m long, erect at the base, arching, growing and leaning on vegetation; internodes lignified, usually hollow, rarely pithy, 5–12 mm thick, glabrous, puberulent, papillose-pubescent, or pubescence reduced to a single line; nodes glabrous, rarely puberulent; sheaths papillose-hispid, with hairs to 3.5 mm long, glabrous or puberulent, the overlapping margin ciliate with hairs 0.5–2.0 mm long, the auricular hairs to 3 mm long; collar puberulent or glabrous, occasionally densely pubescent; ligule usually inconspicuous, (0.3–)0.5–0.8(–1.0) mm long, glabrous or ciliate with hairs to 0.7 mm long; blades ovate, ovate-lanceolate, or occasionally narrowly lanceolate, (4–)6–14(–16) cm long, (1.0–)1.8–4.4(–5.6) cm wide, glabrous, puberulent, pubescent, hispid, or villous, the base asymmetrical, clasping the culm, the margin of the base usually ciliate with hairs 1–3 mm long, sometimes glabrous, the margin scabrid, the apex acute to acuminate; panicles rather dense, (2–)4–16(–22) cm long, the longest branch

1–6(–9) cm long, the lowest three panicle branches widely separated, widely spreading at maturity, scabrous or puberulent, the lower pulvini usually puberulent, sometimes glabrous; spikelet globose (2.6–)2.8–3.8(–4.0) mm long; first glume (1.0–)1.2–2.2 mm long, 9–13-nerved; second glume 11–13-nerved; sterile floret without a staminate flower, the lemma 11–13-nerved; the palea ⅔ to equal the length of the fertile floret; fertile floret 2.8–3.6 mm long, 2.0–2.9 mm wide, dark brown to grayish black, the anthers 1.4–2.3 mm long, white, the stigmas white, the base of the fertile lemma usually with a distinct shelf from which a sterile projection often arises, the palea usually deeply concave; caryopsis 2.0–2.5 mm long, 1.7–2.2 mm wide; chromosome number $n = 18$.

Ecology: *Lasiacis ruscifolia* var. *ruscifolia* is common in dry deciduous forests and scrub forests, coastal thickets, and gallery forests. It is also occasional along wet forest margins and shrub communities. Elevation records are almost all below 1,000 m. The main period of inflorescence production is from June to February.

Distribution: *Lasiacis ruscifolia* var. *ruscifolia* is common in Mexico from Lower Baja California and Sinaloa across Mexico below the northern deserts and south throughout Central America. One collection is known from the United States in southern Florida. In South America, it is known from Colombia, Venezuela, and Ecuador and in the West Indies from Cuba and Jamaica.

In describing *P. liebmannianum* var. *depauperatum* Fournier (1886) listed one collection under subvariety α and two under subvariety β but none under variety *depauperatum* itself. I have chosen the specimen under subvariety α as the lectotype of var. *depauperatum*. All three cited specimens belong with *L. ruscifolia* var. *ruscifolia*.

Lasiacis ruscifolia var. *ruscifolia* is a widespread and variable taxon. It is distinguished by its broad blades, short ligules, and rather dense panicles bearing distinctly globose spikelets. The blades of the main culm are usually broadly ovate and suffice to identify this variety. However, those of the minor secondary branches are often conspicuously narrower. The majority of specimens from Guayas, Ecuador, have soild pithy culms rather than the hollow culms that characterize the species in the other parts of its range.

As a whole, this variety is especially variable in pubescence, but three pubescence types predominate. These are: (1) plants rather prominently puberulent throughout the sheaths and the blades, (2) plants strongly papillose-hispid on the sheaths but glabrous on the blades, and (3) plants glabrous on both sheaths and blades.

Lasiacis ruscifolia var. *ruscifolia* is closely related to *L. sorghoidea* var. *sorghoidea*. The latter species is distinguished most readily by its longer, narrower leaves. It also differs in having a more open panicle with longer branches, bearing narrower, more obovate spikelets than in *L. ruscifolia*. The large majority of Central American and West Indian specimens of *L. sorghoidea* can be effectively distinguished by their distinctive pattern of leaf pubescence. In *L. sorghoidea* var. *sorghoidea*, the upper blade surface is puberulent, the lower surface is velutinous, the collar is densely hispid, and the sheath is conspicuously

papillose-hispid. This combination is only found very rarely in *L. ruscifolia* var. *ruscifolia*.

In South America, especially in Ecuador and Colombia, the two species are not as distinct because *L. sorghoidea* var. *sorghoidea* tends to have wider leaves and denser inflorescences. There I have relied heavily on pubescence characters and assigned all those with the typical *L. sorghoidea* var. *sorghoidea* pattern to that taxon. I have recognized as *L. ruscifolia* var. *ruscifolia*, plants with puberulent sheaths, broad ovate leaves, short inflorescence branches, and distinctly globose spikelets. Although the two taxa seem to merge somewhat in this area, I have continued to recognize them at the species level because they maintain their separate identities throughout the rest of their range of sympatry. Fieldwork in Ecuador and Colombia is needed to fully resolve the evolutionary interaction (if any) between these taxa.

Several morphological types within this polymorphic have received specific recognition.

Lasiacis liebmannianum Fourn. represents a morphological type with narrow, compact panicles in which the panicle branches are strictly appressed to the main inflorescence axis. However, I have seen collections taken from the same plant in which these panicle branches spread at maturity, and I have observed a similar narrow inflorescence as an abnormality in a single greenhouse plant of *L. ruscifolia*. Thus, this morphological type may not have a genetic basis.

Lasiacis globosa Hitchc. was distinguished on the basis of small spikelet size (ca. 3.0 mm). However, measurements of a large number of spikelets from plants throughout the range of the species showed a normal distribution of spikelet size from 2.8 to 3.8 mm, the average of all specimens being 3.3 mm. Therefore, plants with small spikelets occupy the lower end of a continuum, and there is no evident discontinuity to justify taxonomic recognition.

Lasiacis glabra Swallen was considered closely related to *L. ruscifolia* by Swallen (1955b) but was described as a new species on the basis of having elongate, simple or only sparingly branching flowering branches, and being completely glabrous, except for the somewhat ciliate sheaths. However, the lack of pubescence is again an end point of a continuum in pubescence development. Although Swallen stated that *L. glabra* was based on the single holotype collection, Hitchcock (1920) had already noted that glabrous plants of *L. ruscifolia* occur occasionally throughout Central America. They also occur in Mexico and South America. The lack of branching of the flowering culms alluded to by Swallen is definitely only a developmental stage. All vigorous greenhouse plants of *L. ruscifolia* var. *ruscifolia* produce large terminal inflorescences on unbranched culms. After or shortly before the spikelets have matured, the main culm may begin to branch extensively.

BELIZE. BELIZE: Mi 42.5 on Northern Hwy., *Dwyer 11005* (MO). Altun Hua, *Wiley 562* (MO), *564* (MO). CAYO: El Cayo, *Bartlett 11522* (GH, US). Xunanturich, *Rose Innes 192* (ISC). Macaw Bank, *Lundell 6576* (US). CORAZAL: Port Sal, *Gentle 104* (F); *Rose Innes 92* (IJ); *Lundell 4906* (GH, NY, UC, US).

COLOMBIA. ANTIOQUIA: 1 km antes Occidente, *Barkeley et al. 445* (COL, US). 2 km N of Antioquia, *Barkley et al. 17C059* (COL). Alrededores de Antioquia, *Barkeley et al. 17C374* (COL). 1 km antes Occidente, *Scolnik et al. 19An319* (UC, US). ATLANTICO: Entre Palmar

de Varela y Ponedera, *Dugand & Barriga 2440A* (COL, US). Entre Barona y Galapa, *Dugand 5782* (COL). Barranquilla, *Elias 250* (US), *1098* (F, NY, US). BOLÍVAR: Near Cartagena, *Killip & Smith 14082* (COL, GH, NY, US). Cartagena Bay, *Killip & Smith 14126* (F, GH, MO, NY, US). N of Arjona, *Killip & Smith 14513* (GH, NY, US). Vic. de Beltrán, *Romero-Castañeda 9888* (COL). CUNDINAMARCA: Vic. of Apulo, *Killip et al. 38261* (COL, US). MAGDALENA: Hoya del Río Cesar, *Cuatrecasas & Romero-Castañeda 24893* (COL, US), *24922* (COL, US). 20 km NW of La Jagua, *Haught 3633* (COL, US). Pivijay, *Romero-Castañeda 24893* (COL, US), *24922* (COL, US). Pivijay, *Romero-Castañeda 9096* (COL, MO). Santa Marta, *Smith 174* (MO, US, WIS). SAN ANDRÉS ISLAND: *Daniel 5641* (US); *Fernández-Pérez 5194* (COL, US); *Torres 220* (COL). SANTANDER: Vic. of Suratá, *Killip & Smith 16476* (GH, NY, US). Río Zulia, *Molina et al. 18NS052* (US). VALLE: Between Cartago and Alcolá, *Cuatrecasas 22909* (F, US). Palmira, *García-Barriga 18858* (COL).

COSTA RICA. ALAJUELA: Nuestro Amo, *Jiménez 531* (US). Crecia, *Jiménez 1127* (US). Las Ventanas, *León 2926* (US). Río Grande de Tárcoles, *Pohl & Davidse 11355* (ISC). GUANACASTE: Ca. 40 km N of Liberia, *Anderson & Mori 269* (F). Near 27 Abril Rd. to Playa Tamarindo, *Burger & Ramírez 4117* (F, NY, US). Vic. of Cañas, *Daubenmire 169* (F), *438* (F). 40 km N of Cañas, *Davidse 833* (UC). NE of Liberia, *Dodge et al. 6251* (GH). Vic. of Cañas, *Gentry 303* (MO, WIS). W of Bagaces, *Heithaus 307* (MO). Colonia Carmona, *Jiménez 361* (US), *369B* (US), *376* (US). Río Bebedero, *Jiménez 725* (US). Santa Rosa National Park, *Liesner 4241* (MO), *4422* (MO). Taboga, *Pohl & Calderón 9826* (ISC), *10139* (ISC). 21 km N of Liberia, *Pohl & Calderón 10161* (ISC). Ca. 40 km N of Liberia, *Pohl & Calderón 10180* (ISC). Ca. 8 km S of La Cruz, *Pohl & Calderón 10183* (ISC), *10184* (ISC), *10196* (ISC). Vic. of Cañas, *Pohl & Davidse 10541* (ISC, MO), *11335* (ISC). Murciélago, *Pohl & Davidse 11562* (ISC). Vic. of Libano, *Standley & Valerio 44888* (US). Bebedero, *Standley & Valerio 46695* (US). Ca. 8 km S of La Cruz, *Williams et al. 26436* (F, NY, US). Bahía de Sta. Elena, *Williams et al. 26703* (F, NY, US). PUNTARENAS: Southern Nicoya Peninsula, *Burger & Liesner 6583* (F, MO). Near Puntarenas, *Hitchcock 8570* (US), *8571* (US), *8577* (US). Near the Puntarenas jct., *Pohl & Davidse 11278* (ISC). SAN JOSÉ: Isla de Chira, *Valerio 1484* (F).

CUBA. CAMAGÜEY: Palo Seco, *Ekman 15318* (NY, US). ISLA DE PINOS: Columbia, *Britton et al. 14659* (NY, US). Vivijagua, *Britton et al. 15065* (NY, US). Near Nueva Gerona, *Curtis 520* (F, GH, MO, NY, P, US); *Ekman 11721* (F, NY, US). Sierra Las Casas, *Killip 44165* (US). Sierra de Caballos, *Killip 44533* (US). Near Nueva Gerona, *Palmer & Riley 904* (US). LAS VILLAS: Near Sancti Spiritus, *León 905* (US). Banao Mts., *Luna 898* (NY), *1005* (NY). ORIENTE: Ensenada de Mora, *Britton et al. 12979* (NY, US). Santiago, *Clemente 5683* (GH, US). Rioja, *Ekman 4903* (US). Sabanaso, *Ekman 635* (F, NY, US). Near Caney, *Ekman 7681* (US). Between Marimon and Boniato, *Ekman 7699* (US). Coufiaua, *Hioram & Baptiste 1351* (NY). Near Guatánamo, *Hioram 2240* (GH, NY); *León 3778* (NY, US). PINAR DEL RÍO: Vic. of Las Palacios, *Shafer 11684* (NY).

CURACAO. Christoffel Mtn., *Arnoldo 1926* (US); *Stoffers 1184* (A, IJ).

ECUADOR. GUAYAS: Vic. of Guayaquil, *Anthony & Tate 63* (US); *Asplund 5687* (US), *5807* (US). Chongón, *Asplund 5879* (US). Vic. of Guayaquil, *Hitchcock 19963* (GH, NY, US). Between Guayaquil and Salinas, *Hitchcock 20057* (GH, NY, US). Vic. of Guayaquil, *Hitchcock 20125* (US), *20135* (US); *Holway & Holway 801* (US); *Mille 34* (US), *1089* (F); *Solís 20582* (US). ORO: Between Santa Rosa and La Chorita, *Hitchcock 21130* (US).

EL SALVADOR. AHUACHAPÁN: Vic. of Ahuachapán, *Standley & Padilla 2738* (F); *Standley 19870* (GH, MO, NY, US). CHALATENANGO: Near Chalatenango, *Davidse & Pohl 2068* (ISC). LA LIBERTAD: 12 km W of La Libertad, *Davidse & Pohl 2023* (ISC, MO). 15 km W of La Libertad, *Davidse & Pohl 2024* (ISC). N shore of Lago Ilopango, *Davidse & Pohl 2033* (ISC, MO). LA UNIÓN: Vic. of La Unión, *Standley 20660* (GH, US). MORAZÁN: 15 km NE of San Miguel, *Tucker 488* (F, ISC, UC, US). SANTA ANA: E side of Lago Coatepeque, *Davidse & Pohl 2037* (ISC). 6 mi N of Metapán, *Davidse & Pohl 2066* (ISC, MO). Santa Ana, *Hitchcock 8850* (UC, US). 11 km E of Metapán, *Pohl & Erickson 12583* (ISC, MO). SAN MIGUEL: Lolotique, *Cruz Guevara 76* (MO). Vic. of San Miguel, *Standley 21138* (GH, US). SAN SALVADOR: Vic. of San Salvador, *Calderón 67* (GH, NY, US), *510* (NY, US), *861* (US); *Hitchcock 8903* (US). Vic. of Tonacatepeque, *Standley 19421* (GH, US), *19437* (GH, NY, US). Vic. of San Salvador, *Standley 22465* (GH, MO, NY, US). SAN VICENTE: Vic. of San Vincente, *Standley & Padilla 3390* (F), *3673* (F, UC).

GUATEMALA. ALTA VERAPAZ: 15 mi W of Telemán, *Croat 41532* (MO). Alta Verapaz, *Standley 70650* (F). CHIQUIMULA: 3 km S of Quezaltepeque, *Harmon & Dwyer 3697* (MO).

Above Chiquimula, *Standley 74328* (F). Between Ramírez and Cumbu de Chiquimula, *Standley 74531* (F). Chiquimula, *Steyermark 30083* (F, US). Near Jacotán, *Steyermark 31536* (F). EL PROGRESO: 8 km S of El Progreso, *Iltis G-73* (WIS). ESCUINTLA: 12 km W of Escuintla, *Harmon & Fuentes 4684* (MO). Hwy. 2A, *Harmon & Fuentes 4719* (MO). Near Escuintla, *Standley 63929* (F). Near San José, *Standley 64089* (F). Between Masagua and San José, *Standley 64127* (F). HUEHUETENANGO: Between Neutón and Catarina, *Steyermark 51810* (F, US). IZABAL: Vic. of Lake Izabal, *Jones & Facey 3474* (IJ, US); *Snedaker C-47* (F). W of Zapotillo airstrip, *Snedaker D-51* (F). JALAPA: Between Jalapa and San Pedro, *Standley 77080* (F, US). Vic. of Jalapa, *Standley 77392* (F). Between Monjas and Jalapa, *Steyermark 32186* (F). JUTIAPA: Vic. of Jutiapa, *Melhuis & Goodman 3703* (F, ISC); *Standley 74885* (F, US), *75253* (F, US), *75541* (F). Between Jutiapa and Las Tunas, *Standley 76224* (F, US). PETÉN: 2 mi E of Melchor, *Croat 24618* (MO); *Dwyer 11245* (MO). Lake Petén, *Dwyer 11274* (MO). 3 mi W of Melchor, *Gentry 8266* (MO). N of El Cruce, *Gentry 8319* (MO). Lake Petén, *Lundell 3861* (US). Yaxha–Remate, *Lundell 3862* (US). Lake Petén Itza, *Lundell 17240* (US). 35 km E of Santa Elena, *Molina 15430* (F). QUICHE: *Aguilar 1437* (F). RETALHULEU: Between Nueva Linda and Champerica, *Standley 87711* (F, US). Along the Río Coyote, *Standley 88381* (F, US). SAN MARCOS: Near Malacatán, *Standley 68861* (F). SANTA ROSA: Jumaytepeque, *Heyde & Lux 3899* (GH, US). Near Guazacapán, *Standley 78693* (F). SE of Chiquimulilla, *Standley 78784* (F). NE of Chiquimulilla, *Standley 78882* (F). Río La Cruz, *Standley 79009* (F). Vic. of Chiquimulilla, *Standley 79254* (F). SUCHITEPÉQUEZ: Cocales, *Standley 62085* (F, US). Suchitepéquez, *Standley 62192* (F). Vic. of Tiquisate, *Steyermark 47667* (F, US). ZACAPA: Between Río Hondo and Santa Cruz, *Standley 74114* (F). Vic. of Santa Rosalia, *Steyermark 29294* (F).

HONDURAS. ATLANTIDA: La Ceiba, *Alduvín 124* (MO). Lancetillo, *Chickering 9* (US). 9 km E of Tela, *Davidse & Pohl 2188* (ISC, MO). 33 km E of Tela, *Davidse & Pohl 2190* (ISC, MO). 17 km SSE of La Ceiba, *Davidse & Pohl 2198* (ISC, MO). Vic. of Tela, *Mitchell 20* (GH). Lancetilla, *Molina 10392* (F). Vic. of Alejo, *Standley 7705* (F). Vic. of Tela, *Standley 53273* (A, F, US), *54553* (A, F, US), *54779* (A, F, US). Lancetilla, *Williams & Molina 14442* (F, GH). Vic. of La Ceiba, *Yuncker et al. 8226* (F, GH, MO, NY). CHOLUTECA: Vic. of San Marcos de Colón, *Standley 15957* (F). Vic. of Pespire, *Standley 27134* (F). COPÁN: Vic. of Copán, *Molina & Molina 24610* (F, NY), *24779* (F, NY). Between Santa Rita and Titoror Creek, *Molina 30663* (MO). CORTES: 1 km S of Puerto Cortes, *Davidse & Pohl 2169* (ISC, MO). Río Ulua, *Molina 5646* (F). Near Potrerillos, Cortes, *Yuncker 4915* (F, MO). EL PARAÍSO: Ca. 45 km E of Tegucigalpa, *Freytag s.n.* (WIS). Below Guayabille, *Molina 654* (F, GH). Río Yeguare, *Molina 1085* (F, US). 9 km S of Danlí, *Pohl & Gabel 13424* (MO). MORAZÁN: Vic. of El Zamorano, *Davidse & Pohl 2082* (ISC, MO). Río Yeguare, *Glassman 1924* (F, NY). Vic. of El Zamorano, *Molina 1393* (F, US); *Rodríguez 123* (F), *125* (F). Tatumbla, *Rodríguez 525* (F). Río Yeguare, *Rodríguez 981* (F), *997* (F). Vic. of El Zamorano, *Standley 367* (F), *1500* (F, MO), *12159* (F), *15177* (F), *22316* (F, UC), *23581* (UC); *Swallen 10785* (US), *11009* (US), *11159* (US). Río Yeguare, *Williams & Molina 10343* (A, F, MO); *Williams 15956* (US), *16915* (F, GH, MO). OCOTEPEQUE: Vic. of San Antonio, *Molina 22466* (F, NY). OLANCHO: Between San Felipe Catacamas and El Plomo, *Molina 13279* (F). SANTA BÁRBARA: 4 km NE of La Arada, *Harmon & Dwyer 3825* (MO). Vic. of Santa Bárbara, *Molina 22013* (F, MO, NY).

JAMAICA. PORTLAND: Port Antonio, *Millspaugh 984* (F). ST. ELIZABETH: Font Hill, *Britton 1509* (NY). WESTMORLAND: Bluefields, *Britton 1624* (NY).

MEXICO. BAJA CALIFORNIA SUR: Sierra La Giganta, *Carter et al. 2023* (GH, MEXU, UC, US); *Carter & Kellogg 3110* (MEXU, UC, US); *Gentry 4130* (GH, MO, UC). CAMPECHE: Tuxpeña, *Lundell 927* (F, MO, NY, UC, US), *1315* (F). CHIAPAS: Between Tapachula and Puerto Madero, *Beetle M-4021* (MO). Between Escuintla and Mapastepec, *Beetle M-4036* (MO). Between La Trinitaria and El Jocote, *Beetle M-4141* (MO). 11 mi S of La Trinitaria, *Breedlove & Raven 13247* (F). 1 km N of Ocozocoautla, *Breedlove 19803* (MO). Near Rizo de Oro, *Breedlove & Thorne 20654* (MO). NW of Puerto Arista, *Breedlove & Thorne 20875* (MO). 15 km SW of Suchiapa, *Breedlove 28223* (MO). 25–30 km SE of Tonalá, *Breedlove 28329* (MO). 5–6 km NW of Las Cruces, *Breedlove 28449* (MO). 6–8 km NE of Huixtla, *Breedlove 28581* (MO), 28582 (MO). 10 km SE of Mapastepec, *Breedlove & Thorne 30735* (MO). 5 km N of Cintalapa, *Breedlove 36588* (MO). 5 km W of Rizo de Oro, *Breedlove 36707* (MO). Rd. to Nueva Concordia, *Breedlove 37617* (MO), *37636* (MO). 6–8 km E of Frontera Comalapa, *Breedlove 39046* (MO). Ca. 21 mi NE of the Tehuantepec-Tapachula intersection, *Davidse & Davidse 9571* (MO). Zacualapa, *Juzepczuk 1360* (US). Escuinta, *Matuda 2117* (GH, NY, UC, US). Tonalá, *Matuda 16898* (F, MEXU,

MO). Escuinta, *Matuda 17180* (F, MEXU, NY). Tonalá, *Matuda 17204* (F, MEXU). San Fernando, *Miranda 5127* (MEXU). 24 km E of Villa Flores, *Miranda 5952* (MEXU). Berriozábal, *Miranda 6718* (MEXU). Monserate, *Purpus 425* (F, US). 4 km SW of Las Rosas, *Roe et al. 1003* (WIS). 15 km N of Pueblo Nuevo, *Roe et al. 1264* (WIS). Between Sureste and Mal Paso, *Roe et al. 1432* (F, WIS). Mapastepec, *Tateoka 1001* (US), *1032* (US). El Chorreadero, *Ton 2947* (WIS). Acala to Pugiltik, *Ton 3180* (NY). El Chorreadero, *Ton 3269* (NY). N of Mapastepec, *Xolocotzi X-225* (US). CHIHUAHUA: Río Mayo, *Gentry 2402* (F, GH, MEXU, MO, UC, US). Hacienda San Miguel, *Palmer 10* (GH, MEXU, NY, P, US). COLIMA: Between Manzanillo and Minatitlan, *Beetle et al. M-3511* (MO). Paso del Río, *Emrick 15* (F). Manzanillo, *Hitchcock 7027* (F, GH, MO, NY, UC, US), *7028* (US), *7034* (US), *7044* (US). Alzada, *Hitchcock 7079* (F, GH, NY, UC, US), *7087* (F, GH, MO, NY, UC, US). Manzanillo, *Palmer 1089* (GH, MO, NY). DURANGO: Near Huasenate, *Rose 3502* (GH, US). Río Mezquital, *Soule 2130* (MO), *2133A* (MO). GUERRERO: Grutas de Cacahuamilpa, *González 1770* (WIS). Guayameo, *Hinton 9386* (GH, MO, NY). Montes de Oca, *Hinton 11381* (GH, MO, NY, US), *11569* (NY, US). Galena, Atayac, *Hinton 14610* (GH, NY, US). Acapulco, *MacDaniels 166* (F). Temisco, *Mexia 8717* (F, GH, MO, NY, UC, US). Puerto Marque, *Miranda 8421* (MEXU). Acahuitzotla to Acapulco, *Moore 5107* (GH, UC, US). Tlalixtaquilla, *Nelson 2254* (GH, US). Almoloya–Teloloapan–Iguala, *Sohns 966* (US). HIDALGO: Vic. of Huejutla, *Moore 2207* (GH). JALISCO: La Barranca, *Bárcena 138* (MEXU). S of Ciudad Guzmán, *Beetle et al. M-3437* (MO). Between Autlán and Bajia de Navidad, *Beetle el al. M-3564* (MO), *M-3567* (MO), *M-3575* (MO). 14 km SW of Puerto Vallante, *Carter & Chisoki 1261* (UC). Guadalajara, *Hitchcock 7368* (US). Near Río Grande de Santiago, *Leavenworth & Leavenworth 1901* (F, GH, MO, NY). 10–16 mi NE of Autlán, *McVaugh 19756* (NY), *19778* (NY). 16 mi SW of Autlán, *McVaugh 19975* (NY), *19981* (NY). 8 km NW of Barra de Navidad, *McVaugh 20761* (NY). Between Bahía Navidad and La Manzanilla, *McVaugh 21022* (NY, UC). 2 mi above La Cuesta, *McVaugh 21144* (GH, NY, UC, WIS). 2 km SE of Puerto Vallarta, *Rzedowski 17729* (US). SE de Puerto Vallarta, *Rzedowski 17758* (US). MÉXICO: Temascaltepec, *Hinton 1767* (GH, MEXU, US), *4847* (NY, US). Otzoloapan, *Matuda 31445* (MEXU, MO). Tlatlaya, *Matuda 32100* (MEXU). MICHOACÁN: Aguila, *Hinton 16121* (IJ, NY, US). 32 km N of Playa Azul, *King & Soderstrom 4925* (MEXU, NY, UC, US). 4 mi NW of Apatzingán, *McVaugh 17925* (NY, US). 75 km from El Tamascal, *Moore et al. 5665* (GH, UC, US). 8 km NW of Aguila, *Rzedowski 17932* (US). MORELOS: Cuernavaca, *Leavenworth & Leavenworth 913* (F). Xochiltepec, *Lyonnet 2172* (US). Cañon de Lobos, *Miranda 1654* (MEXU). Near Yautepec, *Pringle 11293* (F, GH, MEXU, MO, NY, US). NAYARIT: Near San Blas, *Alva & Cook 1608* (UC). 15 km W of Ahuacatlán, *Feddema 518* (US). Vic. of San Blas, *Ferris 5322* (US). Tres Marias Isl., *Ferris 5656* (MO, US). Vic. of Jalisco, *Ferris 5848* (GH, MEXU, US). 19 mi NW of Tepic, *McVaugh & Koelz 722* (US). E of Tepic, *Pennell 19961* (MEXU, US). 1 km N of El Cuatante, *Rzedowski 17880* (US). NUEVO LEÓN: 20 km NW of Montemorelos, *Weaver 1005* (GH, US). OAXACA: Between Acayucan and Tehuacán, *Beetle M-3114* (MO). 18 mi W of Jct. Mex. 147 and Mex. 185, *Brunken & Perino 286* (MO), *288* (MO). Inchitán, *Conzatti 3697* (MEXU). Tepenix Tlahuaca, *Conzatti 4370* (MEXU). Costa Chica, *Kaplan & Kaplan 170AX55* (F, GH, MEXU). Vic. of Concordia, *Morton & Makrinius 2441* (F, US). Ca. 132 km S of Oaxaca, *Norris & Taranto 16501* (MO). 9 km S of Matías Romero, *Pohl & Davidse 11821* (ISC, MO). Temascalpa to San Ildefanso de Villa Alto, *Santos 3534* (NY, US). Tuxtepec, *Sousa 743* (MEXU). PUEBLA: Matamoros, *Miranda 2375* (MEXU). Huachinango, *Salazar 5* (MEXU). Villa Juárez, *Sarukhán 1476* (MEXU). Between México and Tuxpan, *Sarukhán 2918* (MEXU). QUINTANA ROO: Tancah, *Swallen 2808* (MEXU, US), *3816* (US). SAN LUIS POTOSÍ: Vic. of Tamazunchale, *Carlson 2772* (F). El Bonito, *Chase 7544* (GH, US). Vic. of Tamazunchale, *Edwards 478* (MO, UC, US). 11 mi W of Ebano, *Johnston & Crutchfield 5679* (US). Vic. of Xilitla, *Kenoyer A599* (F). Vic. of Tamazunchale, *Kenoyer 1017* (F, MO); *Lundell & Lundell 7251* (US). 15 km S of Antiguo Morelos, *Norris 17427* (MO). Near Xolol, *Pohl & Davidse 11808* (ISC, MO). Vic. of Salto de Agua, *Sohns 1408* (US), *1417* (US). Hwy. 55 to Xilitla, *Sohns 1436* (US). SINALOA: Vic. of Mazatlan, *Barr & Mason 64-12* (UC). Vic. of Culiacan, *Brandegee s.n.* (US). Above Cofradia NE of Imala, *Breedlove 35586* (MO). Vic. of Labadras, *Ferris & Mexia 5141* (F, GH, US). Imala, *Gentry 4981* (GH, MO, NY, US). Cerro Llano Redondo, *Gentry 7097* (F, GH, NY, UC, US), *7097A* (GH, NY, UC, US). La Noria, *Mexia 187* (UC). Elota, *Ortega 5901* (GH, US). Vic. of Mazatlan, *Ortega 813* (MEXU). Cacalotan, *Ortega 1005* (MEXU). Vic. of Mazatlan, *Ortega 4330* (US), *5973* (US). Chametla, *Ortega 6459* (GH, US). Závalo, *Ortega 7487* (MO). Mazatlán, *Rose et al. 14112* (US). Acaponeta, *Rose et al. 14409* (US). Vic. of

Rosario, *Rose et al. 14521* (NY, US). SONORA: Alamos, *Drouet & Richards 3945* (F, US). Mescales, Río Mayo, *Gentry 2290* (US). Guasaremos, *Gentry 2402* (US). SE of Ciudad Obregon, *Gentry 14525* (US). Sierra de Alamos, *Rose et al. 12822* (US). 8 mi NE of Matapa, *Wiggins & Collins 430* (GH, MO, NY, UC, US). 18 mi SE of Magdalena, *Wiggins 7148* (GH, US). 10 mi N of Ures, *Wiggins 7351* (US). TABASCO: 21 km W of Cardenas, *Conrad & Conrad 2966* (MO). La Palma to Balancan, *Matuda 3292* (F, GH, MEXU, US). Teapa, *Rovirosa 573* (NY). TAMAULIPAS: Vic. of Marmolejo, *Bartlett 10796* (GH, ISC, MEXU, US). S of Mante, *Elias et al. 7* (A). Tampico, *Fischer 46193* (US). 2 mi N of Antigua, *Graham & Johnston 4411* (MEXU). 5 mi N of San Rafael, *Johnston & Crutchfield 4957* (MEXU). 35 mi S of Victoria, *Johnston 5754* (US). Tampico, *Kenoyer 1021* (F, MO). 22.5 km from Manuel, *Martínez & Luyando F159* (US). Jaumave, *Rozynski 76* (F, UC). Chamal, *Swallen 1639* (US), *1709* (US). VERACRUZ: 25 mi SE of Xalapa, *Barkley et al. 2625* (MEXU). Cabañas, *Bravo 218* (MEXU). Alemán Cosamaloapan, *Calderón 1094* (MEXU, MO). Tlalixcoyan, *Calderón 1561* (MEXU, MO). San Lorenzo Tenochtitlan, *Chavelas et al. ES-2657* (MEXU). Ciudad Alemán Cosamaloapan, *Delgadillo 1094* (MO). Barra Platanar, *Dorantes et al. 1281* (MO). E of San Andrés Tuxtla, *Dressler & Jones 5* (GH, MEXU, MO, NY, UC, US). El Jicacal, *Gómez-Pompa 4881* (MEXU). Chavarillo, *Johnson s.n.* (US). Palmar, *McDaniels 876* (F). Misantla, *Purpus 5978* (F, GH, MO, NY, P, US). Zacuapan, *Purpus 7877* (GH, MO, NY, US). 1 mi E of Santiago Tuxtla, *Reeder & Reeder 4333* (US). Goyame, *Rosas 1375* (A, MEXU). Zacuapan, *Rozynski 620* (F). Near Sontecomapan, *Rzedowski 20342* (MEXU). Veracruz-Jalapa Rd., *Soderstrom 459* (US). Plan del Río, *Ventura 4198* (WIS). San Antonio, *Woronow 2182* (US). Paso de Ovejas, *Xolocotzi X-3371* (US). YUCATÁN: Uxmal, *Beetle M-935* (ISC, US). Mayacan, *Beetle M-957* (WIS). Near Kabah, *Beetle M-3814* (MO). Chichen Itza, *Bequaert 53* (A). Calotmul, *Gaumer 2141* (F). Chichankanab, *Gaumer 2461* (F, GH, P, NY). Oxmal, *Iltis 27278* (MO, WIS). Chichen Itza, *Millspaugh 11639* (F). Valladalid to Tizimín, *Miranda 133* (MEXU). Uxmal, *Rzedowski 26343* (WIS). Mérida, *Schott 600* (F, US); *Seler 3835* (F). Chichen Itza, *Steere 166* (US), *1299* (US), *Swallen 2398* (US), *2418* (US). Tizimín, *Swallen 2514* (US). Uxmal, *Swallen 2635* (US). Peto, *Swallen 2694* (US), *2717* (MEXU, US).

NICARAGUA. BOACA: Boaca, *Seymour 3841* (F, GH, MO, NY, WIS). CARAZO: Jinotepe, *Hitchcock 8676* (US), *8715* (US), *8719* (US). CHINANDEGA: Corinto, *Hitchcock 8743* (US). Potosí, *Marshall & Neill 6608* (MO). CHONTALES: From Juigalpa NE toward La Libertad, *Stevens 4041* (ISC, MO). Ca. 2.8 km N of Cuapa, *Stevens 6061* (MO); *Vincelli 68* (MO). ESTELÍ: 4 mi S of Estelí, *Dwyer et al. 446* (MO). GRANADA: Volcán Mombacho, *Dudley & Moore 1948* (NY). LEÓN: Quesalguague, *Baker 2105* (GH, MO, US). Poneloya, *D'Arcy 10401* (MO). Along the Río Sinecapa, *Stevens 3845* (MO). MANAGUA: Vic. of Managua, *Chaves 409* (US). 27 km S of Managua, *Davidse & Pohl 2379* (ISC, MO). Vic. of Managua, *Garnier 41* (US), *408* (US), *A-1241* (GH, US), *1490* (F, US), *1550* (GH, WIS), *1551* (GH, WIS), *4558* (GH, WIS); *Maxon et al. 7546* (GH, US). Río Santa Clara, *Neill 2875* (MO). Masachapa, *Nichols 1363* (MO). Tipitapa, *Seymour 2831* (MO). Km 11 on Hwy. 12, *Stevens 4756* (MO). MASAYA: Lake Masaya, *Atwood 3289* (F, GH, MO, NY). Masaya, *Hitchcock 8710* (US). Parque Nacional Volcán Masaya, *Neill 2843* (MO); *Stevens 5275* (MO). MATAGALPA: Matagalpa, *Molina 22843* (F, NY). Hwy. to Matagalpa, *Molina 22858* (F, NY). NUEVA SEGOVIA: 3 km W of Ocotal, *Atwood 761* (GH, NY); *Seymour 845* (GH, MO, NY). RIVAS: Km 142 Route 2, *Hamblett 1874* (NY). San Juan del Sur, *Hitchcock 8607* (US).

PANAMA. CANAL ZONE: Río Abajo, *Bartlett & Lasser 16397* (MO). Beyond Fort Amador, *D'Arcy 9262* (MO). Ft. Kobbe, *D'Arcy 9619* (MO). Madden Dam, *Ebinger 858* (MO, US). Balboa, *Hitchcock 8060* (US). Between Panamá and Corozal, *Hitchcock 9204* (US). Gutuncillo, *Piper 5272* (US). Balboa, *Standley 25258* (US), *25438* (US), *26077* (MO, US), *29318* (MO), *32134* (US). Farfan Beach area, *Tyson 1806* (MO, US). Fort Amador, *Tyson 2012* (MO). Madden Lake, *Witherspoon & Witherspoon 8801* (MO). CHIRIQUÍ: Burica Peninsula, *Busey 574* (MO). COCLÉ: Penonemé, *Conte 15* (MO). 20 mi S of Nata, *Croat 9642* (MO). Río Penonomé, *Henriquez 14* (MO). La Pintada, *León 25* (MO). Aguadulce, *Lezcano 26* (MO); *Pittier 4987* (US), *4998* (F, GH, US). HERRERA: Pesé, *Allen 797* (F, GH, MO, NY, US). Río Santa Maria, *Burch et al. 1187* (MO, UC). LOS SANTOS: 5 mi S of Pocrí, *Croat 9739* (MO). Las Tablas, *Dwyer 2529* (MO, US). Vic. of Tonosí, *Stern et al. 1865* (MO, US). PANAMÁ: Taboga Island, *Allen 137* (GH, MO, US), *1290* (GH, MO, NY, US). Trapeche Island, *Allen 2624* (MO, US). Taboga Island, *Celestius 47* (US). Río Oharco–Espiritu, *Duke 5702* (MO). Isla de la Bayonetia, *Dwyer 1752* (US). San José Island, *Harlow 73* (GH, US). Pacora, *Hertentains 13* (MO). Taboga Island, *Hitchcock 8068* (US). Vic.

of Panamá, *Hitchcock 8401* (UC, US). San José Island, *Johnston 162* (GH, US), *187* (US), *1255* (US). Bella Vista, *Killip 4040* (NY). Taboga Island, *Killip 4157* (US). Bella Vista, *Killip 12011* (GH, NY, US). Chimán, *Lewis et al. 3328* (MO, UC). Taboga Island, *Macbride & Featherstone 2788* (F, GH, NY, US). San José Island, *Miller 1895* (MO). Taboga Island, *Mori & Kallunki 4075* (MO); *Pittier 3603* (US). Chepo, *Pittier 4688* (NY). Matías Hernández, *Pittier 6892* (US). Bella Vista, *Standley 25302* (US). Near Panamá, *Standley 26890* (US). Taboga Island, *Standley 27017* (US), *27870* (US). Punta Paitilla, *Standley 30807* (US), *30809* (US); *Sucre 123* (MO). Taboga Island, *Tyson & Loftin 5150* (SCZ). VERAGUAS: Camino a Santa Fé, *Cisneros 20* (MO). Puerto Mutis, *Tyson 6028* (MO, SCZ).

UNITED STATES. FLORIDA: Manatee Co., Terra Ceia Island, *Beckner 794* (WIS).

VENEZUELA. ANZOÁTEGUI: 21 km E of Piritu, *Davidse 5020* (MO). ARAGUA: Maracay, *Cárdenas 456* (MO, NY). 19 km NW of Rancho Grande, *Davidse 3120* (ISC, MO). 2.5 km S of Cata, *Davidse 3125* (ISC, MO). Vic. of Taiguaiguai, *Fernández 444* (MO, NY). Maracay, *Montaldo s.n.* (MY). Ocumare de la Costa, *Williams 12182* (F, VEN). CARABOBO: Punta Palmita, *Benítez de Rojas 365* (MO, NY). Near El Palito, *Pittier 7686* (GH, US, VEN). Valencia to El Paíto, *Trupillo s.n.* (MY). Isla del Burro, *Vareschi 1905* (VEN). COJEDES: Río Pao, Paraima, *Trujillo 5442* (NY). GUÁRICO: 16 km SSW of Calabozo, *Davidse 2944A* (MO). 14 km N of Dos Caminos, *Davidse 3012* (ISC, MO). 15 km SW of Tamaco, *Davidse 4220* (MO). San Juan de los Morros, *Fernández 1409* (MY). LARA: Río Turbido, *Fernández 922* (MY). Alrededores de Barquisimeto, *Trujillo 7533* (MY). MIRANDA: La Moka, *Eggers 13480* (US). 2 km NW of Carenero, *Steyermark & Bunting 102299* (VEN). YARACUY: Camino de Oroa, *Curran 309M* (VEN). ZULIA: Cerca Mene Grande, *Pittier 10617* (GH, NY, US, VEN).

12b. **Lasiacis ruscifolia** (H.B.K.) Hitchc. var. **velutina** (Swallen) Davidse, Ann. Missouri Bot. Gard. 64: 375. 1978.

Lasiacis velutina Swallen, Ceiba 4: 288. 1955. TYPE: Honduras, Morazán, vicinity of El Zamorano, road to San Antonio, 17 Oct. 1951, *Swallen 10834* (US, holotype).

Perennial; culms caespitose, 1–6 m tall, erect at the base, arching or leaning on vegetation; internodes 3–7 mm thick, lignified, hollow, glabrous or with a line of puberulence; nodes glabrous; sheaths pilose or velutinous, the overlapping margin and throat ciliate, the auricular hairs 2–3 mm long; collar pilose; ligule 0.2–0.6(–1.0) mm long, ciliolate, inconspicuous; blades ovate to ovate-lanceolate, 2–7(–9.5) cm long, 0.8–2.8 cm wide, the upper surface hispid to velutinous or pilose, the lower surface softly long pilose, the base asymmetrical, the basal segment clasping the culm and ciliate, the apex acute to acuminate; panicles 4–13 cm long, the longest branch 2–7 cm long, the lower portion of the panicle included in the sheath or exserted, the branches ascending or spreading somewhat, pilose or pubescent, the pulvini usually pilose; spikelets subglobose, 3.5–4.0 mm long, usually purple when immature; first glume 1.5–2.3 mm long, 9–11-nerved; second glume 11–15-nerved; sterile floret with a staminate flower, the anthers 2.4 mm long, the lemma 9–13-nerved, the palea subequal the length of the fertile floret; fertile floret 3.2–3.8 mm long, 2.1–2.5 mm wide, the anthers 2.2–2.3 mm long, white, the stigmas purple; caryopsis 2.2 mm long, 1.7 mm wide; chromosome number $n = 18$.

Ecology: This variety is found in brushy borders, moist thickets, and among trees of oak and oak-pine mountain forests from 700 to 1,300 m. Spikelet-bearing plants have been collected from June through December.

Distribution: *L. ruscifolia* var. *velutina* has been found only in central Honduras and northern Venezuela.

The distinctive pilose or velutinous pubescence, usually purple spikelets and

relatively small, broad leaves characterize this taxon. In many respects, it seems intermediate between *L. ruscifolia* var. *ruscifolia* and *L. nigra*. In its subglobose spikelets and ovate blades, it resembles *L. ruscifolia* var. *ruscifolia*. In its pubescence, more open inflorescences, and usually purple spikelets, it resembles the pilose form of *L. nigra*. It does not seem unreasonable to speculate that this variety represents a stabilized hybrid derivative between the two species. Such a hypothesis is amenable to experimental verification, but this has not yet been possible because of difficulty in growing *L. nigra* in the greenhouse.

I have tentatively assigned four Venezuelan specimens from the Distrito Federal to this variety. Chase, as indicated by her annotations, considered these to be late branching forms of *L. ruscifolia* var. *ruscifolia*. However, it is possible that the small leaves of these plants represent genetically fixed characters as they do in the Honduranian representatives of var. *velutina*. The similar inflorescences, purple spikelets, and pubescence (which is, however, less fully developed in *Fernández 127*) strengthens the resemblance to the Central American representatives of var. *velutina*. Since both *L. ruscifolia* var. *ruscifolia* and *L. nigra* occur in Venezuela, it is possible that these plants originated through independent hybridization and stabilization.

HONDURAS. DISTRITO CENTRAL: Between Suyapa and Tegucigalpa, *Molina 1811* (F, GH, US). EL PARAÍSO: Ca. 45 km E of Tegucigalpa, *Freytag s.n.* (WIS). Río Yeguare, *Molina 4051* (F, GH, US). MORAZÁN: Between San Antonio and El Zamorano, *Davidse & Pohl 2162* (ISC, MO). Vic. of El Zamorano, *Freytag 3184* (WIS); *Glassman 1732* (F, NY). Carretera Suyapa, *Molina 12837* (US). 8 km de Santa Rosa de Copán, *Molina 12880* (US). Río Rancho Quemado, *Molina 18631* (F, GH, NY). Vic. of El Zamorano, *Pohl 12508* (ISC, MO). Chagüite, *Rodríguez 384* (F). Río Yeguare, *Rodríguez 832* (F). El Pedegral, *Rodríguez 895* (F). Río Yeguare, *Standley 1056* (F). Vic. of El Zamorano, *Standley 1694* (F), 2289 (F). Río de la Orilla, *Standley 24173* (F, GH, NY, UC, US). El Jicarito, *Standley 24863* (F). Río Agua Amarilla, *Standley 26683* (F, GH, ISC, MO, US), *26686* (F, GH). Santa Inés, *Williams & Molina 10407* (F, GH, MO, NY). Río Yeguare, *Williams 16928* (F, GH, ISC, MO, WIS).

VENEZUELA. DISTRITO FEDERAL: Falda del Cerro de Pasaynaca, El Valle, *Fernández 5* (VEN), *127* (VEN). Hacienda Sosa, *Tamayo 496* (VEN), *2010* (VEN).

13. **Lasiacis scabrior** Hitchc., Proc. Biol. Soc. Wash. 40: 85. 1927. TYPE: Guatemala, Alta Verapaz, Cubilqüitz, an Waldrandern, hoch klimmend, Feb. 1913, *von Tuerckheim 4036* (US-725618, holotype; US-727020, isotype).

Perennial; culms caespitose, erect or arching and clambering over vegetation, 1–6 m tall; internodes to 13 mm thick, hollow, lignified, papillose-pubescent or puberulent especially at the apex or pubescence reduced to a line; nodes glabrous; sheaths commonly pubescent or villous with hairs to 2 mm long, sometimes becoming glabrate, the overlapping margin and throat ciliate with hairs usually 2.0–3.5 mm long; collar glabrous or with a definite line of pubescence at its base; ligule a conspicuous, usually dark brown, lacerate membrane (3.5–)4.0–6.0(–7.0) mm long, glabrous or appressed pubescent on the back, one margin usually prominently ciliolate with hairs to 3.0 mm long; blades elliptic-lanceolate to linear-lanceolate, (6–)8–12(–16) cm long, 1.0–2.2(–3.0) cm wide, the upper surface scabrid and/or puberulent along the midrib, especially toward the base, the lower surface usually densely puberulent, less commonly glabrate, the base asymmetrical, the apex acuminate, the margin scabrid; panicles (1–)4–9 cm long,

nearly spherical, the longest branch (1–)2–5 cm long, spikelet density moderate, the base of the panicle always included in the upper sheath, numerous inflorescences usually developed on the secondary branches, without a large terminal inflorescence, the branches spreading to slightly reflexed, usually pubescent or densely puberulent below, scabrid above, the pulvini puberulent to pubescent, the pedicels widely divergent at maturity; spikelets (3.5–)3.7–4.1(–4.5) mm long, obovoid; first glume (1.2–)1.7–2.0(–2.8) mm long, 7–11-nerved; second glume 9–13-nerved; sterile floret without a flower or with the rudiments of a staminate flower, the lemma 11–13-nerved, the palea ⅔ to subequal the length of the fertile floret; fertile floret 3.5–3.6 mm long, 1.8–2.0 mm wide, dark brown, with a depression on the dorsal surface, the anthers ca. 2 mm long, white, the stigmas white; caryopsis 2.1–1.3 mm long, 1.4–1.6 mm wide.

Ecology: *Lasiacis scabrior* is a plant most frequently found in clearings, along trails, and margins of wet forests. It is a grass of low to middle elevations, 0–1,100 m. The majority of spikelet-bearing plants in Central America have been collected from January to the middle of April. In the southern part of the range, they have been primarily collected later in the year.

Distribution: *Lasiacis scabrior* is known from Oaxaca and Veracruz, Mexico south through Central America, to Colombia, Ecuador, and Peru.

Lasiacis scabrior is a distinctive species, most easily recognized by its long ligules and many small, nearly spherical inflorescences that are always included in the upper sheaths. The ligule is the longest of all the erect, woody species and well surpasses those of *L. ligulata*. The inflorescence character is very distinctive. Inflorescences in all other species may occasionally be included in the sheaths, but then it is probably caused by environmental conditions. In *L. scabrior*, it is genetically fixed. *Lasiacis standleyi* also has very long ligules similar in appearance to those of *L. scabrior*. However, *L. scabrior* has large inflorescences well exserted from the sheaths. The two species have similar leaf morphology, culm pubescence, and, as already noted, ligules. On this basis, I believe these two species to be related. They probably form the closest link between the creeping and erect species of any *Lasiacis* species pair. Among the erect species, the affinity of *L. scabrior* probably lies with *L. ligulata*.

Common name: British Honduras: El Cayo, reed, *Gentle 9023*.

BELIZE. CAYO: 47 mi sect. Hummingbird Hwy., *Gentle 9023* (F, IJ, UC, US). TOLEDO: Monkey River, *Gentle 4398* (US). Edwards Rd. beyond Columbia, *Gentle 6366* (F, IJ, NY, UC).

COLOMBIA. ANTIOQUIA: Cerca Villa Arteaga, *Soto & Barkley 18C541* (COL). CAQUETÁ: Florencia, *Perez 673* (COL, US). CHOCÓ: Hydro Camp 8, *Duke 15311* (MO). Hydro Camp 6, *Duke 15342* (MO). Bahía Solano, *Killip & Garcia 33554* (COL, US), *33594* (COL, US). VALLE: Río Digua, *Cuatrecasas 13674* (F, GH, MO).

COSTA RICA. ALAJUELA: 8 km NE of Villa Quesada, *Molina et al. 17294* (US). 2 km W of La Marina, *Molina et al. 17385* (F, NY). 6–8 km S of Villa Quesada, *Molina et al. 17480* (F, UC, WIS). CARTAGO: Vic. of Turrialba, *Godfrey 66178* (US). Vic. of Pejivalle, *Standley & Valerio 47117* (US). GUANACASTE: N of Tilarán, *Standley & Valerio 45897* (US). HEREDIA: 3 km SE of Puerto Viejo, *Opler 1644* (MO). Sarapiquí, *Brolley 7465* (M, US). LIMÓN: La Lola, *Carlson 3277* (F). 6 km W of Guápiles, *Pohl & Calderón 10019* (ISC). Vic. of Guápiles, *Standley 37178* (F). Río Yurquím, *Tonduz 8527* (GH, M, US). PUNTARENAS: Palmar Sur de Osa, *Allen 5870* (ISC). 5 km W of Rincón de Osa, *Burger & Gentry*

8812 (MO). 1 mi SW of Cañas Gordas, *Croat 22274* (MO). Las Cruces, *Croat 44409* (MO). Río Agua Buena, *Liesner 1988* (MO). Near San Vito de Java, *Pohl & Davidse 10791* (ISC). 3 km NE of Quepos, *Pohl & Davidse 11692* (ISC). Between Golfo Dulce and Río Térraba, *Skutch 5391* (ISC, US). SAN JOSÉ: Vic. of San Isidro del General, *Molina et al. 18111* (F). *Pittier 3365* (US); *Skutch 2155* (GH, MO, NY, US), *3871* (GH, NY, US). PROVINCE UNKNOWN: Rodeo de Paca, *Pittier 3245* (US). Shirones, *Tonduz 9213* (US). Tsaki, *Tonduz 9492* (F, US).

ECUADOR. CHIMBORAZO: Naranjapata, *Schimpff 526* (A, F, MO). ESMERALDAS: Guadual, *Solís 12433* (F). GUAYAS: 3 km W of Bucy, *Hitchcock 20438* (US), *20523* (US). LOJA: Santiago to Zamora, *Camp 1119* (NY, US). MANABI: *Haught 2973* (UC, US). NAPO: Cerro Antisana, *Grubb et al. 1521* (US). PICHINCHA: Vic. of Santo Domingo de los Colorados, *Cazalet & Pennington 5125* (NY, UC, US); *Fagerlind & Wibon 1594* (MO); *Solís 13889* (US).

EL SALVADOR. AHUACHAPÁN: Sierra de Apaneca, *Standley 20109* (GH).

GUATEMALA. ALTA VERAPAZ: 6 km NWW of Sebol, *Contreras 4270* (US). 2.5 mi W of Cubilqüitz, *Steyermark 44350* (F). HUEHUETENANGO: Vic. of Ixcán, *Steyermark s.n.* (F). PETÉN: Trail to Tenosique, *Contreras 3327* (US).

HONDURAS. ATLANTIDA: 28 km NE of El Progreso, *Davidse & Pohl 2173* (ISC, MO). OLANCHO: Río Wampú, *Nelson & Clewell 0699* (MO).

MEXICO. CHIAPAS: Río Usumacinta, *Breedlove 33955* (MO). Río Ixcán, *Breedlove & McClintock 34090* (MO). OAXACA: Tolosito, *Williams 9572* (F, US). VERACRUZ: Hidalgotitlán, *Avendano & Avendano 13* (MO); *Dorantes 2703* (MO). Coatzacoalcos River, *Williams 8615* (F, US), *8960* (F, US).

NICARAGUA. GRANADA: Volcán Mombacho, *Baker 2454* (MO, UC, US). RÍO SAN JUAN: 20 km NE of El Castillo, *Neill & Vincelli 3573* (MO). ZELAYA: 1 mi N of Ocongwas, *Englesing 194* (F, MO, US). Colonia La Esperanza, *Vincelli 140* (MO). Colonia Manantiales, *Vincelli 231* (MO). S of Cerro Bacan, *Vincelli 311A* (MO).

PANAMA. CANAL ZONE: 12 mi from Gamboa Gate, *Croat & Sharp 13950* (MO). CHIRIQUÍ: Burica Peninsula, *Croat 22169* (MO). 1 mi E of Cañas Gordas, *Liesner 267A* (MO). COCLÉ: El Valle de Antón, *Allen 1641* (F, GH, MO, NY), *2061* (F, GH, MO, NY). Vic. of La Mesa, *Allen 2376* (US). Cerro Pilón, *Dwyer et al. 4549* (MO). Above El Valle, *Gentry 6897* (MO). 44 km N of Penomé, *Hammel 1672* (MO). 16.7 km N of Llano Grande, *Hammel 1872* (MO). COLÓN: Vic. of Río Indio, *Croat 33667* (MO). DARIÉN: Agua Fria, *Duke 10098* (MO). Mannera to mouth of Río Cuasí, *Kirkbride & Bristan 1553* (MO, NY). Vic. of Campamento Buena Vista, *Stern et al. 851* (GH, MO), *920* (GH, MO). LOS SANTOS: Azuero Peninsula, *Croat 34474* (MO). 11 mi N of Tonosí, *Tyson et al. 2977* (MO). PANAMÁ: Cerro Azul, *Calderón 2091* (US). Cerro Jefe, *Duke 9442* (MO); *Dwyer et al. 3511* (MO), *3514* (MO); *Dwyer 8479* (MO); *Gentry & Dwyer 3511* (MO). Cerro Campana, *Ebinger 340* (MO, US). San José Island, *Johnston 548* (GH, MO, US). Rd. from El Llano to Cartí-Tupile, *Kennedy & Dressler 2953* (MO). 5 mi SW of Cerro Brewster, *Lewis et al. 3376* (COL, MO, UC). Cerro Campana, *Porter et al. 4271* (MO). Cerro Jefe, *Tyson et al. 3327* (MO). Cerro Campana, *Wilbur & Weaver 11289* (MO). VERAGUAS: NW of Santa Fé, *Mori & Kallunki 4881* (MO). 6–7 km N of Santa Fé, *Nee 9778* (MO).

PERU. HUÁNUCO: Vic. of Tingo Maria, *Mathias & Taylor 3463* (US). LA MAR: Dept. Ayacucho, *Dudley 10025* (MO). LORETO: Inchua, *Soukup 3022* (F, US). SAN MARTIN: 8 km above San Antonio, *Belshaw 3615* (F, GH, MO, NY, UC, WIS).

14. **Lasiacis sloanei** (Griseb.) Hitchc., Bot. Gaz. (Crawfordsville) 57: 302. 1911.

Panicum latifolium Hamilt., Prodr. Pl. Ind. Occ. 10. 1825, non *P. latifolium* L. 1753. TYPE: Antilles, (ex. spec. Hort. Paris) Desvaux herbarium (P).

P. sloanei Griseb., Fl. Brit. W. Ind. 551. 1864. TYPE: Jamaica, Manchester, woods near Broken(horn?), Nov. 1843, *Purdie s.n.* (K, lectotype).

P. divaricatum Presl ex Griseb., Fl. Brit. W. Ind. 551. 1864, non *P. divaricatum* L., 1759, cited as a synonym of *P. sloanei* by Grisebach (1864).

Perennial; culms caespitose, erect, clambering, or climbing, 1–6 m long; internodes hollow, 4–10 mm thick in mature culms, the young leafy internodes usually with a line of puberulence, otherwise glabrous; nodes glabrous; sheaths

glabrous, ciliate on the upper margin and the throat, the auricular hairs 1.5–3.0 mm long; collar often extended somewhat, forming a pseudopetiole to 3 mm long, usually densely puberulent or short-hispid with hairs to 1.5 mm long; ligule membranous, 0.5–0.8(–1.0) mm long, ciliolate with hairs 0.3–0.6 mm long, occasionally ciliate with hairs to 1.5 mm long, the back of the ligule puberulent, rarely glabrous; blades 8–16(–18) cm long, (1.3–)1.7–4.0(–4.5) cm wide, ovate to ovate-lanceolate or lanceolate, the upper surface puberulent or scabrous at the base of the midrib or often nearly the entire length of the midrib, otherwise shiny and glabrous, the lower surface glabrous, the base asymmetrical, the apex usually abruptly acuminate, the margin scabrid; panicles 6–34 cm long, open with relatively few, short-pedicelled spikelets appressed to the inflorescence branches, the longest branch 2–15 cm long, the main branches spreading, the upper branches ascending to spreading, scabrid, the lower pulvini sometimes puberulent, otherwise glabrous; spikelets (4.0–)4.3–4.8(–5.3) mm long; first glume (1.5–)1.7–2.4(–2.6) mm long, 7–9-nerved; second glume 9–13-nerved; sterile floret with or without a staminate flower, the anthers 1.5–2.0 mm long, occasionally only rudimentary, the lemma 9–13-nerved, palea ¾ to nearly as long as the fertile floret; fertile floret 3.8–4.3 mm long, 2.2–2.6 mm wide, the anthers 1.8–2.2 mm long, white, the stigmas white; caryopsis 2.3–2.6 mm long, 1.8–2.0 mm wide, whitish; chromosome number $n = 18$.

Ecology: *Lasiacis sloanei* is primarily a species of moist, forest edges. It may also be found in recently deforested areas, shrubby secondary growth, and thickets along roadsides and fence rows. It usually occurs at low elevations. All but one record, from Tamaulipas, Mexico, are from below 1,000 m. In southern Tamaulipas, it has apparently been collected up to 1,450 m. Spikelet-bearing plants have mostly been collected from July to March, although a few specimens have been collected in the intervening months as well.

Distribution: *Lasiacis sloanei* extends from southern Tamaulipas, Mexico, south throughout Central America. I have seen no specimens from Panama and El Salvador, although the species probably occurs in both countries. In South America, this species is known from Colombia, Venezuela, and from only one collection from Ecuador. In the West Indies, it occurs on the major islands of the Greater Antilles, Cuba, Jamaica, and Hispaniola, as well as the smaller islands of Antigua in the Leeward Islands.

Panicum sloanei was described by Grisebach on the basis of two collections (*Purdie* and *Wullschlaegel* 872) from Jamaica. A lectotype has never been chosen. Consequently, I have selected the Purdie specimen at Kew as the lectotype. I have also seen a specimen of the *Wullschlaegel* syntype from GOET, and this is also referable to *L. sloanei*.

Although Hitchcock (1920) stated that Grisebach based *Panicum sloanei* on Sloane's plate (Voy. Jam. 1: *tab. 71, fig.* 3. 1707) as well as the two aforementioned collections, it is more probable that Grisebach based the description on the specimens only and that he considered the specimen figured in Sloane's plate to be conspecific with *P. sloanei*. This interpretation was made by Dr. Stearn (pers. comm.) of the British Museum and is almost certainly correct since

Grisebach in the Introduction to his Flora stated that he drew up his descriptions from actual specimens and "it is but rarely that I have copied from others." Both the *Purdie* and the *Wullschlaegel* specimens have glabrous upper and lower blade surfaces, and Grisebach (1864) described *P. sloanei* as having glabrous leaves. Moreover, Dr. Launert, agrostologist at the British Museum, reports (pers. comm.) that the Sloane specimen (Herb. Sloane 2 fol. 36), upon which the Sloane plate is based, has both surfaces covered with a fine pubescence. This is further evidence that this specimen was not used by Grisebach in drawing up the description of *P. sloanei.* Dandy (1958) also noted that Grisebach had apparently not used the Sloane Herbarium in writing the Flora of the British West Indies. No pubescence is illustrated in the Sloane plate. This suggests that Grisebach examined only the plate and on this basis identified the specimen as *P. sloanei.* The plate also shows that the specimen has small spikelets and a much branched inflorescence with widely spreading pedicels. All these characteristics suggest that the specimen upon which the plate is based is not *L. sloanei,* as Hitchcock (1908) suggested, but rather *L. sorghoidea.* It is clear, therefore, that Sloane's plate and specimen do not have any value in typification of the name *P. sloanei,* even though the specific epithet suggests a connection between Sloane's plate and the taxon *L. sloanei.*

Quite a different interpretation has been made by Baum (1967) in his discussion of the application of the name *Panicum latifolium* L. Baum designated Sloan's specimen (BM) upon which Sloanes's plate was based as the holotype for *P. sloanei.* According to Baum: "The other syntype [i.e. for *P. latifolium*] is Sloane. jam. 34. hist. 1. p. 114, t. 71. f. 3, which was identified by Hitchcock as *P. sloanei* Griseb.; however, Grisebach (1864) seems to have based his new species, *P. sloanei,* on *P. latifolium jamaicense* L., which is actually Sloane's element." I have already noted that Grisebach almost certainly based his description on the two specimens from Jamaica, and on this basis, we can dismiss Baum's typification of *P. sloanei.*

On the basis of Hamilton's (1825) description of *Panicum latifolium,* I have followed Hitchcock & Chase (1917) in assigning this binomial to synonymy under *Lasiacis sloanei.* I have not seen the type which is presumably in Paris.

Lasiacis sloanei is characterized by glabrous sheaths and blades that are broad, shiny, and glabrous except for a line of puberulence or scabridity along the midrib on the upper surface. This species also has a collar that is densely puberulent or hispid, and the inflorescence is sparsely flowered with large spikelets born on short pedicels appressed to the panicle branches. The pubescence pattern of the leaf is very constant and is one of the least variable of all *Lasiacis* species. It serves as an excellent vegetative identification characteristic.

Lasiacis sloanei is most closely related to *L. divaricata. Lasiacis divaricata* has shorter and narrower leaves that typically lack the characteristic pubescence pattern of *L. sloanei,* smaller spikelets, smaller panicle branches that become conspicuously reflexed at maturity, pedicels that diverge widely from the panicle branches, and vigorous young culms that grow in a zigzag pattern when branching.

Occasional specimens of *L. divaricata* may duplicate the leaf pubescence

pattern of *L. sloanei*, but these can be distinguished by the other characters. Also, profusely branched plants of *L. sloanei* may rarely approach *L. divaricata* in leaf size but may be correctly identified by the other diagnostic characters.

ANTIGUA: NE of Dark Valley, *Box 119* (US).

BELIZE. BELIZE: Gracie Rock, *Croat 23912* (MO). CAYO: 41 mi Hummingbird Hwy., *Gentle 8980* (F, IJ, NY, UC, US). El Cayo, *Lundell 6433* (F, GH, NY, US). Ca. 1 mi S ot Hummingbird Hwy., *Spellman & Newey 1661* (MO). Ca. 1 mi S of Belmopan, *Spellman & Newey 1888* (MO). ORANGE WALK: Honey Camp, *Gentle 555* (GH, MO, NY, US). TOLEDO: Cero, *Gentle 6966* (US).

COLOMBIA. CUNDINAMARCA: La Vega, *García-Barriga 10638* (US). MAGDALENA: Parque Nacional Tayrona, *Kirkbride 2496* (MO). Don Amo, Santa Marta, *Smith 2145* (F, GH, MO, NY, P, US, WIS). META: Río Cüejar, *Smith & Idrobo 1534* (COL, GH, ISC, MO, NY).

COSTA RICA. CARTAGO: Turrialba, *Pittier 9056* (US); *Pohl & Calderón 10300* (ISC); *Tonduz 8319* (M, US). GUANACASTE: 30 km N of Cañas, *Pohl 12637* (US).

CUBA. CAMAGÜEY: Palo Seco, *Ekman 15319* (US). HABANA: Loma Esperá, *Ekman 653* (K). Camoa Hills, *León 766* (US). Sierra de Anafe, *León 1967* (GH). Near Cojímar, *León 1973* (US). Jamaica, *León 2603* (GH), *13657* (GH). Sierra de Anafe, *León 16670* (GH). LAS VILLAS: Vic. of Cienfuegos, *Brues s.n.* (GH, NY); *Combs 55* (F, GH, ISC, K, MO, NY, P). Vic. of Soledad, *Howard 6250* (GH, NY, US). Amaro, *León & Loustalot 9444* (NY). Vic. of Cienfuegos, *Jack 5187* (F, GH, NY); *Linder s.n.* (GH). MANTANZAS: Vic. of Mantanzas, *Britton et al. 115* (F, NY); *Britton & Wilson 121* (NY), *393* (NY); *Britton et al. 586* (NY). Boca de Canasí, *León 13171* (GH, US). Vic. of Mantanzas, *Rugel 868* (NY). ORIENTE: Mayarí Arriba, *Ekman 15851* (US). Ubero River, *Taylor 328* (NY). PINAR DEL RÍO: Loma San Gabriel, *Ekman 10557* (NY). E of Mariel, *Ekman 12853* (F, NY, US). Sierra Mendoza, *Ekman 13657* (GH). La Güira, *León 4563* (GH, US). Sierra de los Organos, *Morton 4441* (US). Sierra Mendoza, *Shafer 11147* (NY, US). Sierra de Anafe, *Wilson 11421* (NY, US).

DOMINICAN REPUBLIC. EL SEIBO: La Romana, *Ekman H12094* (GH, K, NY, US). SAN PEDRO DE MACORÍS: 23 km W of San Pedro de Marcoris, *Howard & Howard 9508* (GH, NY, US).

ECUADOR. Recreo, *Eggers 15553* (F).

GUATEMALA. PETÉN: Uaxactum, *Bartlett 12129* (ISC, US), *12199* (US). Dos Lagunas, *Contreras 1518* (IJ, US), *1689* (US). Uaxactum, *Contreras 3641* (US). Tikal, *Contreras 3683* (US), *3746* (US), *3911* (US); *Lundell 15785* (IJ, US), *16146* (US), *17150* (IJ, US). Lake Petén Itza, *Lundell 17239* (US). Tikal, *Molina 15818* (US). QUETZALTENANGO: Colomba, *Skutch 1345* (GH, US).

HAITI. GONAVE ISLAND: Anse Galette, *Leonard 3105* (GH, IJ, NY, US), *3240* (F, GH, NY, US). Vic. Etroite, *Leonard 3290* (F, GH, IJ, NY, US). Vic. of Pikmi, *Leonard 5121* (NY, US). L'ARBONITE: Vic. of Emmery, *Leonard 9466* (MO, US). L'OUEST: Port-au-Prince, *Ekman 2190* (GH, IJ, US). Pétionville, *Leonard 4883* (IJ, NY, US), *5024* (GH, IJ, US), *5054* (GH, IJ, US). NORD OUEST: Haut Pibon, *Ekman 4438* (GH, US). St. Louis du Nord, *Leonard & Leonard 14292* (GH, NY). SUD: Grand Riviere de Jeremie, *Bartlett 17498* (US). Between Anse d'Hainautt and Dame Marie, *Bartlett 17519* (US).

HONDURAS. Swan Islands, *Nelson 13* (GH). COMAYAGUA: Comayagua, *Hernández 5279* (MO). COPÁN: 4 mi E of Copán Ruins, *Molina 30776* (MO). CORTES: Río Piedras, *Molina 3541* (F, GH, MO, US). 5 km de San Pedro Sula, *Molina 3814* (F, GH, MO, US). YORO: 19 km SE of Río Viejo, *Davidse & Pohl 2200* (ISC, MO).

JAMAICA. CLARENDON: Round Hill, *Proctor 9480* (IJ). HANOVER: Green Island, *Britton & Hollick 2128* (NY). PORTLAND: 6 mi W of St. Margaret's Bay, *Wright 118* (F, NY). ST. ANDREW: Gordon Town, *Barry s.n.* (IJ). Vic. of Kingston, *Britton 2996* (NY). Below Chestervale, *Davidse & Proctor 3249* (ISC, MO). Robertsfield, *Harris 11376* (NY). Gordon Town to Flamstead, *Harris 11454* (F, GH, IJ, K, MO, NY, P, US). Bryan's Hill, *Harris 11531* (F, NY, US). Constant Spring, *Hitchcock A.G.N.H.590* (GH, MO, NY, P, US). Bog Walk, *Hitchcock s.n.* (MO); *Maxon 10502* (NY, US). Gordon Town, *Patrick 187* (IJ). ST. ANN: 14 mi S of Ocho Rios, *Davidse & Conroy 3273* (ISC, MO). ST. CATHERINE: Between Bog Walk and Spanish Town, *Hitchcock A.G.N.H.591* (F, GH, K, MO, NY, P, US). Ewarton to Linstead, *Hitchcock 9413* (US). Near Lluidas Vale, *Hunnewell 15226* (IJ). Linstead, *Hunnewell 19752* (IJ). ST. ELIZABETH: Ipswich to Black River, *Hitchcock 9606* (US). S of Gutters, *Howard & Proctor 13818* (GH, IJ). ST. JAMES: Near Montego Bay, *Maxon & Killip 1673* (F, GH, NY, US); *Ridley 35* (US). ST. THOMAS: 2.4 mi SE of Cedar Valley,

Davidse & Conroy 3264 (ISC, MO). TRELAWNY: Near Troy, *Harris 12614* (GH, K, MO, NY, US); *Hitchcock 9801* (US).

MEXICO. CAMPECHE: Tuxpeña, *Lundell 904* (F, GH, MEXU, MO, US). CHIAPAS: 50 km SW of Palenque, *Beetle M-3906* (MO). 6–12 km S of Palenque, *Breedlove 28849* (MO). 3 km W of the Chiapas-Tabasco border, *Conrad & Conrad 2986* (MO). N of Chapulhuacan, *Moore 1328* (GH, UC, US). OAXACA: 5 km S of Tuxtepec, *Conrad & Conrad 3253* (MO). 8 mi NE of Valle Nacional, *Davidse & Davidse 9732* (MO). Tuxtepec, *Miranda 4233* (MEXU). NE of Chiltepec, *Santos 3834* (NY, US). QUINTANA ROO: Tancah, *Swallen 2807* (US), *2817* (US). SAN LUIS POTOSÍ: Tamazunchale, *Fischer 37129* (GH, MO, NY, US); *Kenoyer s.n.* (MO); *Leavenworth & Leavenworth 1945* (MO, US); *Lundell & Lundell 7125* (MEXU, NY, US). Tamasopo, *Pennell 18012* (GH, US); *Pringle 3403* (US). 48 km W of Valles, *Roe et al. 203* (WIS). 52 km W of Valles, *Roe et al. 2236* (WIS). Narango–Salta de Agua, *Sohns 1395* (US), *1406* (US). TAMAULIPAS: Santa Maria de Nogales, *Martínez & Luyando F2102* (US). 18 km NW of Ocampo, *Stanford et al. 1061* (GH, MO, NY, UC, US). VERACRUZ: Sapoapan de Cabañas, *Bravo 250* (MEXU). Papantla, *Rzedowski 23370* (MEXU, WIS). YUCATÁN: Chichen Itzá, *Beetle 885* (ISC); *Swallen 2415* (US). Tizimín, *Swallen 2519* (US). Peto, *Swallen 2692* (US), *2714* (MEXU, US), *2719* (US).

NICARAGUA. CARAZO: Jinotepe, *Hitchcock 8673* (US), *8700* (US). CHONTALES: 12 km E of Villa Somoza, *Davidse & Pohl 2388* (ISC, MO). MANAGUA: Sierra de Managua, *Garnier 1531* (US).

VENEZUELA. ARAGUA: 16.3 km NW of Rancho Grande, *Davidse 3116* (ISC, MO). BOLÍVAR: El Pao Viejo, *Davidse et al. 4969* (MO). E of Miamo, *Steyermark 88189* (NY, VEN, US). DISTRITO FEDERAL: Sosa, *Tamayo 563* (VEN). LARA: Near Barquisimeto, *Saer 280* (NY, P, VEN, US). MÉRIDA: Rd. to Mijagual, *Tillett & Hönig 738-549* (MO).

15a. **Lasiacis sorghoidea** (Desv.) Hitchc. & Chase var. **sorghoidea**, Contr. U.S. Natl. Herb. 18: 338. 1917.

Panicum lanatum Swartz, Prodr. Veg. Ind. Occ. 24. 1788, non *P. lanatum* Rottb., 1776. TYPE: Jamaica, *Swartz s.n.* (S, holotype, fragment US, photograph US).

P. glutinosum Lam., Tabl. Encycl. 1: 74, *tab. 43, fig. 3.* 1791, non *P. glutinosum* Swartz, 1788. TYPE: "Amer. Merid. Insula Franciae," (P, not seen).

P. sorghoideum Desv. in Hamilt., Prodr. Pl. Ind. Occ. 10. 1825. TYPE: Porto Rico, Desvaux Herbarium No. 24 (P, holotype).

P. orinocense Willd. ex Spreng., Syst. Veg. 1: 316. 1825, pro syn. TYPE: Venezuela, Orinoco, *Humboldt*, Willdenow Herbarium (B, not seen).

P. arborescens Sieb. ex Trin., Gram. Pan. 208. 1826, "arborscentis," pro syn., non *P. arborescens* L., 1753. TYPE: Martinique, *Sieber 267* (GOET, P).

P. divaricatum L. var. *latifolium* Schlecht. & Cham., Linnaea 6: 33. 1831. TYPE: not indicated, but Mexico, *Schiede & Deppe s.n.* (MO) is *L. sorghoidea* var. *sorghoidea*; also cites "*P. orinocense* Hb. W. 18766, fol. 2.3 [B, not seen], *P. maculatum* Rchb. in Weigelt pl. Surin. exs. [not seen], *P. fuscum* Sieb. fl. Mart. exs. n. 29 [GOET, MO, P, US], *P. airoides* Sieb. Agrost. no. 120 (e nova Holandia?!)" [P], the latter two collections are *L. sorghoidea* var. *sorghoidea*.

P. maculatum Reichb. ex Schlecht. & Cham., Linnaea 6: 33. 1831, pro syn., non *P. maculatum* Aubl., 1775.

P. agglutinans Kunth, Enum. Pl. 1: 120. 1833, based on *P. glutinosum* Lam.

P. divaricatum L. var. *lanatum* Schlecht. & Cham., Linnaea 6: 33. 1831. TYPE: Jamaica, Willdenow Herbarium 18760 (B, not seen).

P. fuscum Sieb. ex Presl, Abh. Böhm. Ges. Wiss. 3: 550. 1845, pro syn. TYPE: Martinique, Flora Martin. no. 29, *Sieber* (GOET, lectotype, chosen by Hitchcock, 1920; MO, P, US, isolectotypes).

P. praegnans Steud., Pl. Glum. 1: 74. 1854. TYPE: Mexico, Oaxaca, *Buchinger s.n.* (P, lectotype, chosen by Hitchcock, 1920, fragment US, photograph US).

P. lanatum Swartz var. *sorghoideum* (Desv.) Griseb., Fl. Brit. W. Ind. 551. 1864.

P. fuscum Sieb. ex Griseb., Fl. Brit. W. Ind. 552. 1864, pro syn.

P. martinicense Griseb., Fl. Brit. W. Ind. 552. 1864, based on *P. fuscum* Sieb. ex Presl. 1845.

P. guaraniticum Speg., Anales Soc. Ci. Argent. 16: 107. 1883. TYPE: Argentina, Misiones, Posadas, March 1883, *von Gulich s.n.* (LPS, holotype, not seen).

P. divaricatum var. *agglutinaus* (Kunth) Hack. ex Sodiro, Anales Univ. Centr. Ecuador 1889: 5. 1889.

P. swartzianum Hitchc., Contr. U.S. Natl. Herb. 12: 140. 1908, based on *P. lanatum* Swartz.
Lasiacis swartziana (Hitchc.) Hitchc., Bot. Gaz. (Crawfordsville) 51: 302. 1911.
L. guaraniticum (Speg.) Parodi, Notas Mus. La Plata, Bot. 8: 95. 1943.
L. acuminata Swallen, Mem. New York Bot. Gard. 9: 267. 1957. TYPE: Venezuela, Territorio Amazonas, Great Rapids of the Orinoco, Isla Carestía at Saltos Carestía y Galio, 5 km north of Sanariapo, 100–200 m, erect to 2 m, 11 Nov. 1953, *Maguire, Wurdack & Bunting 36171* (US, holotype; NY, isotype).

Perennial; culms caespitose, 1–10 m long, erect at the base, often vigorous, arching and leaning on surrounding vegetation; internodes lignified, 5–15 mm thick, hollow, glabrous, papillose-pubescent or pubescence reduced to a single line; nodes glabrous; sheath often papillose-pubescent especially toward the apex, with hairs commonly 1.5–3.5 mm long, also puberulent or pubescent, rarely glabrate, the overlapping margin and throat ciliate, commonly with cilia 2–3 mm long, the auricular hairs usually 2.5–3.5 mm long; collar densely hispid or pilose, occasionally the hairs less prominent; ligule usually inconspicuous (0.3–) 0.5–1.5(–2.6) mm long, usually ciliate with hairs 0.5–1.0(–1.5) mm long; blades elliptic-lanceolate, lanceolate, or linear-lanceolate, rarely ovate-lanceolate, (6–) 9–19(–23) cm long, (0.6–)1.2–3.4(–4.6) cm wide, the upper surface usually puberulent, rarely more heavily pubescent, the lower surface usually velutinous, less commonly puberulent, the base often asymmetrical and often ciliate, the margin scabrid, the apex acuminate; panicle usually large and prominent, (5–)9–25(–35) cm long, the branches usually ascending, spreading at maturity, usually scabrous and/or puberulent or pubescent, the pulvini glabrous to pubescent; spikelets obovate to elliptic, usually purple when immature, (3.0–) 3.4–4.1(–4.3) mm long; first glume (1.2–)1.5–2.1(–2.7) mm long, 7–11-nerved; second glume 9–13-nerved; sterile floret without or with a staminate flower, the anthers 1.7–2.0 mm long, the lemma 9–11-nerved, the palea ½ to equal the length of the fertile floret; fertile floret 2.9–3.8 mm long, 1.7–2.3 mm wide, dark brown, indented on the dorsal surface of the lemma, the anthers 1.9–2.3 mm long; caryopsis 1.8–2.3 mm long, 1.6–1.8 mm wide; chromosome number $n = 18$.

Ecology: *Lasiacis sorghoidea* var. *sorghoidea* is most commonly found along forest edges, brushy slopes, roadsides, hedgerows, and similar secondary communities. Plants have most commonly been collected at elevations below 1,000 m, but occasionally collections have been made up to 1,800 m. Inflorescence production, especially in Central America and the West Indies, starts later (October) than in most species in the genus. Spikelet-bearing plants have usually been collected from October through May.

Distribution: This is the most common and widely distributed species in the genus. It extends from Oaxaca and Veracruz through Central and South America to Jujuy, Chaco, and Corrientes in Argentina and Rio Grande do Sul in Brazil, and in the West Indies throughout the Greater and Lesser Antilles.

See Excluded Species and Names for a discussion of *L. maculata*.

This variety is distinguished by its large, relatively long and narrow blades, pubescent sheaths, short ligules, large, rather open spreading inflorescences, usually purple spikelets, and fertile florets indented on the dorsal surface. The

plants are coarse, large, and usually have large culms which can support themselves in an upright position more easily than in any other species.

As in the majority of *Lasiacis* species, pubescence is quite variable; however, one pattern predominates throughout the range of this variety. In this type, the sheaths are papillose-hispid, the collar is densely hispid, the lower blade surface is velutinous, and the upper blade surface is puberulent to hispidulous. Beginning in the West Indies and becoming more prevalent in northwestern South America, the pubescence, especially of the sheaths, becomes less prominent, and plants with puberulent sheaths and blades may be found. In other respects, these plants confirm to *L. sorghoidea* var. *sorghoidea*. I have also noted that in Venezuela, *L. sorghoidea* tends to have narrower leaves than in most areas. Those from the Territorio Amazonas have been described as a separate species, *L. acuminata*, by Swallen (1957). These plants have more open inflorescenses, and it is possible that they should eventually be recognized as a separate variety. The relationship of var. *sorghoidea* with *L. ruscifolia* var. *ruscifolia* is taken up under that variety.

Many plants from Peru, Ecuador, and western Brazil tend to have longer ligules (1.5–2.6 mm) than plants from the northern part of the range. These plants can generally be distinguished from *L. ligulata* by their larger blades, larger inflorescences with erect to spreading, but not reflexed, branches, and usually heavier pubescence. They may be stabilized hybrid derivatives from hybridization between these species.

Most of the specimens from Paraguay and Argentina have somewhat denser inflorescences than those from the northern parts of the range. It was largely on this basis that Parodi assigned these to *L. guaranitica*. In other ways, these plants resemble *L. sorghoidea*. Consequently, I have not recognized *L. guaranitica*.

Hitchcock took a much broader view of this variety and included *L. nigra*, a separate species in this treatment.

Common names: British Honduras: Stann Creek, wild rice, *Gentle 1910*; El Cayo, rat rice, *Gentle 2196*. Costa Rica: San José, cañuela, *Jiménez 3717*. Ecuador: tundilla, *Solís 5216*. Argentina: Misiones, picauilla, *Montes 2232*; tacuapí, *Montes 2198*.

ARGENTINA. CHACO: Fontana, *Meyer 3861* (F, GH). CORRIENTES: 4 km E de Paso de la Patria, *Arbo et al. 745* (MO). Estancia Santa Teresa, *Petersen 1717* (GH, MO, NY, US). Itati, *Schinini & Mroginski 4515* (MO). Ricón Ombú Chico, *Schinini et al. 11258* (MO). Río Parana y Ayo. San Juan, *Schinini & Quarín 11540* (MO). El Perichón, *Quarín 3388* (MO). FORMOSA: Laishi, *Jörgensen 2875* (GH, MO, NY, US). 28 km al NW de Pirané, *Krapovickas et al. 19544* (MO). Puesto Porteño, *Morel 2479* (US). 2 km N de Puesto Porteño, *Morel 2505* (US). Ruta 86 al Norte, *Morel 5783* (US). Costa Alegre, *Morel 7088* (US). Pilagé, *Morel 7415* (US). 2 km NE of Suerte Angelito, *Morel 7897* (US). 2 km de la frontera, *Morel 8404* (US). Laguna Verá, *Morel s.n.* (US, WIS). JUJUY: Caliligua, *Hunziker 1975* (GH, US). MISIONES: Puerto Leoni, *Cabrera et al. 243* (US). Alto Paraná, *Ekman 617* (US). Loreto, *Ekman 619* (US). Caraguatay, *Montes 1592* (US). La Mina–San Juan, *Montes 2198* (F, US). Puerto Aguirre, *Parodi 4410* (US). Santa Ana, *Rodríguez 258* (GH, NY, US). San Juan, *Schwindt 297* (US, WIS). Mineral, *Schwindt 683* (ISC, MO).

BELIZE. CAYO: Below El Cayo, *Bartlett 11960* (US). El Cayo, *Bartlett 12954* (GH, NY, US). Vaca, *Gentle 2196* (F, GH, US). STANN CREEK: Stann Creek-Mullin's River Rd., *Gentle 1910* (GH, NY, US). Near Hope Creek, *Gentle 7873* (F, IJ, NY, UC). Sapan Rd., *Gentle 8118* (F, IJ, NY, UC, US). 12 mi sect., Stann Creek-Middlesex Rd., *Gentle 9331*

(F, UC, US). TOLEDO: 15 mi sect., Punta Gorda-San Antonio Rd., *Gentle 6945* (F, NY, UC, US).

BOLIVIA. COCHAMBA: Vic. of Cochamba, *Bang 1289* (F, GH, ISC, MO, NY, US), *1291* (US). Espiritu Santo, *Buchtien 161* (F, GH, MO, NY). Cochamba, *Buchtien 2500* (US). LA PAZ: Mapiri, *Buchtien 10* (NY, US), *88* (US). Polopolo bei Coroico, *Buchtien 3635* (MO, US). Millugaya, *Buchtien 4271* (GH, NY, US). San Antonio bis Mapiri, *Buchtien 6442* (US). Chuluman, *Hitchcock 22652* (US). SANTA CRUZ: E of Puerto Suarez, *Chase 11154* (US). Ascensión de Guarayos, *Krapovickas & Schinini 31748* (MO). Canton Buena Vista, *Steinbach 1931* (GH, US), *5551* (F, GH, NY), *7111* (F, GH, MO, NY, UC, US). San Juan, *Williams 960* (NY).

BRAZIL. ACRE: Bôa Vista, *Black 51-12665* (US). AMAPÁ: Rd. to Amapá, *Pires & Cavalcante 52138* (MO, US), *52169* (MO, US). AMAZONAS: Tabatinga, *Pires & Black 852* (RB, US). BAHIA: Ca. 4 km N of Barreiras, *Irwin et al. 31599* (MO). CEARÁ: Crato, *Swallen 4354* (US). DISTRITO FEDERAL: Parque Nacional de Gama, *Clayton 4977* (NY). 10 km S of Brasilia, *Irwin et al. 12268* (US). 3 km S of Sobradinho, *Irwin et al. 15453* (US). Catetinho, *Sucre 310* (RB). GOIÁS: 2 km W of Monte Alegre de Goiás, *Anderson 6950* (MO). Serra do Caiapó, *Anderson 9491* (MO). Ca. 17 km S of Goiás Velho, *Anderson 9923* (MO, RB). Serra Dourada, *Irwin et al. 11884* (MO). Araguaína, *Irwin et al. 21180* (MO, US). Goiás, *Macedo 3734* (US). MARANHÃO: Fazenda Vitoria, *Pires & Black 16962* (NY). Barra do Gorda to Grajahu, *Swallen 3623* (US). Carolina, *Swallen 3888* (RB, US). MATO GROSSO: Ca. 30 km ENE of Barra do Garças, *Anderson 9777* (MO). Ca. 5 km N of Barra do Garças, *Anderson 9878* (MO). Tres Lagos, *Chase 10753* (US). Vic. of Dourados, *Chase 10986* (GH, MO), *11019* (GH, US). Corumbá, *Chase 11129* (F, US). Santa Rita do Araguaya, *Chase 11821* (NY, RB, US). 30 km S of Xavantina, *Harley & Souza 11074* (MO, RB, US). 85 km from Xavantina, *Hunt & Ramos 5673* (NY, US). Serra do Roncador, *Irwin et al. 16309* (MO, US). Ca. 96 km S of Xavantina, *Irwin et al. 17395* (MO, US). Novos, *Kuhlmann 1748* (RB). Poaia territoria, *Lindman 3185* (US). Cuyabá, *Malme 1544B* (US), *1723* (GH, US). Corumbá, *Malme 3053* (GH, US). Rondonopolis, *Kuhlmann 2565* (RB). Ca. 270 km N of Xavantina, *Ratter et al. 2120* (MO, RB). Munic. de Maracajú, *Sucre 10498* (RB). MINAS GERAIS: 2 km from Mendanha, *Anderson 8787* (MO). Serra do Espinhaço, *Anderson et al. 36296* (MO). Between Uberlandia and the Rio Paranahyba, *Chase 11618* (US). Visçosa, *Kuhlmann 162* (RB). Santa Luzia, *Roth 1202* (RB). 7 km S of Belo Horizonte, *Williams & Assis 7136* (F, GH, MO, NY, UC, US). PARANÁ: Barra da Felicidade, *Hatschbach & Haas 16608* (MO, UC). Umuarama, *Hatschbach 13301* (F). Parque Nacional de Iguaçú, *Pereira 5374* (RB, US). Cascavel, *Rambo 53497* (US). RIO DE JANEIRO: Reserva Florestal de Itatiaia, *Braga 2465* (MO). San Pedro, *Chase 10152* (US). Rio de Janeiro, *Delforge s.n.* (RB). Petrópolis, *Sucre & Braga 2649* (MO). SÃO PAULO: Itapira, *Hoehne 20294* (GH, US). Campinas, *Novaes 1237* (US), *1238* (US); *Santoro 617* (US).

COLOMBIA. AMAZONAS: Between Marco and Leticia, *Black & Schultes 4651* (US). Loretoyaca River, *Schultes 6006* (GH). ANTIOQUIA: Vic. of Medellín, *Alfaro 31* (US). Sonsón, *Archer 399* (US). Fredonia, *Archer 522* (US). Granja de las Mercedes en Venecia, *Barkley & Gutiérrez 1652* (US). Vic. of Dabeiba, *Barkley & Gutiérrez 1816* (UC, US), *1831* (US). San Luis de Cocorna, *Castañeda 10076* (NY). Between Argelia and Alto de Tigre, *Core 805* (US). Peñas Blancas, *Juzepczuk 4616* (US). Malena, *Pennell 3776* (NY). Fredonia, *Tomas 892* (US). Vic. of Medellín, *Toro 100* (NY), *399* (US). ATLANTICA: Los Pendales, *Dugand & Barriga 2548* (US); *Dugand 4195* (US). BOLÍVAR: Vic. of Turbaco, *Killip & Smith 14681* (GH, NY, US). Sincelejo, *Pennell 4062* (NY, US). Frasquillo, *Pennell 4605* (NY, US). CALDAS: Pueblo Rico, *Sneidern 5224* (US). CAQUETÁ: Sucre, *Cuatrecasas 9085* (US). 55 km SE of Guadalupe, *Davidse et al. 5629* (MO). 10 km SW of Belen, *Davidse et al. 5690* (MO). 8 km SW of San Juan del Fragua, *Davidse et al. 5727* (MO). Morelia, *Soderstrom 1407* (US). CHOCÓ: Río San Juan, *Cuatrecasas 16936* (F, US). Andagoya, *Killip 35492* (US). Mun. de Río Sucio, *León 643* (MO). CUNDINAMARCA: *Cuatrecasas 9624* (US). 20 km NW of Villavicencio, *Davidse & Llanos 5522* (MO). 8 km de Apulo, *Forero & Garzón 269* (MO). 15 km NW of Guaduas, *Gentry et al. 18122* (MO). Below Cachipay, *Gutiérrez 128* (NY, US). Fusagasuga, *Juzepczuk 5388* (US). N of Apulo, *Killip et al. 38230* (US). Perrero, *Woronow & Juzepczuk 4868* (US). HUILA: Mun. de Garzón, *Bermudez 34933* (F, MO). 6 km SE of Altamira, *Davidse et al. 5585A* (MO). 10 km SE of Guadalupe, *Davidse et al. 5605* (MO). MAGDALENA: Camino de la Gran Via a San Pedro, *Romero-Castañeda 10663* (MO). Santa Marta, *Smith 2147* (MO), *2148* (F, GH, MO, NY, P, US), *2258* (ISC, MO, P), *2531* (F, GH, NY). META: Río Meta, Cubarral, *Cuatrecasas*

4447 (US). Villavicencio, *Cuatrecasas 4516* (F, US). Entre ríos Ariari y Meta, *Cuatrecasas 7815* (F, US). E of Puerto López, *Davidse & Llanos 5469* (MO). 4 km NW of Villavicencio, *Luteyn et al. 4799* (MO). NORTE DE SANTANDER: Near Río Zulia, *Barkley et al. 18NS070* (US). Confluence of Río Cabugón and Cabaria, *Cuatrecasas 13144* (US). Between Chinacota and La Esmeralda, *Killip & Smith 20901* (US). PUTUMAYO: Piñuña Neguro, *Cuatrecasas 10699* (F, US). SANTANDER: Between Nariño and El Tambor, *Killip & Smith 14952* (US). N slope of Mesa de los Santos, *Killip & Smith 14992* (F, GH, NY, US). Near Bucaramanga, *Killip & Smith 16211* (GH, NY, US). NW of Bucaramanga, *Killip & Smith 16302* (GH, NY, US). Río Magdalena, *Pennell 3916* (F, GH, MO, NY, US). TOLIMA: Libano, *Pennell 2936* (NY, US), *3225* (NY), *3237* (GH, MO, NY, US), *3296* (NY). 5 km W of Chaparral, *Smith 1295* (GH, ISC, UC, US). VALLE: Río Digua, *Cuatrecasas 15069* (F, US). La Cumbre, *Cuatrecasas 19617* (F, US). Río Cali, *Cuatrecasas 18626* (F, US). Cali, *Cuatrecasas 25693* (US). Ansermanuevo, *Forero et al. 3587* (MO). N of Palmira, *García-Barriga 6458* (US). Cali, *Fosberg 21990* (US). Cisneros, *Killip 35542* (US). E of Zarzal, *Pennell et al. 8567* (GH, NY, US), *8573* (GH, US). VICHADA: Ca. 8 km E of Las Gaviotas, *Davidse & Llanos 5165* (MO). Ca. 35 km E of Las Gaviotas, *Davidse & Llanos 5198* (MO). VAUPÉS: Near Miraflores, *Grasel 10047* (US).

COSTA RICA. ALAJUELA: La Calera de San Ramón, *Brenes 6432* (F). Carrillos de Poás, *Brenes 14620* (F, NY). Entre Itiquis y Poás, *Brenes 17331* (F, NY). Carrillos de Poás, *Brenes 17382* (F, NY), *19416* (F, NY). Valley of the Río Itiquis, *Pohl & Davidse 12544* (ISC, MO). CARTAGO: Vic. of Pejivalle, *Skutch 4631* (F, GH, NY, MO, US). Atirro, *Smith 4991* (GH, US). Vic. of Pejivalle, *Standley & Valerio 46876* (US), *47060* (US), *47168* (US). GUANACASTE: Santa Rosa National Park, *Liesner & Lockwood 2416* (MO). Nicoya, *Tonduz 13755* (GH, US). PUNTARENAS: Near Quepos, *Burger et al. 10554* (MO). Osa Peninsula, *Cufodonti 180* (US); *Godfrey 66850* (US). Boruca, *Pittier 4455* (US). SAN JOSÉ: 5 km SW of San Isidro, *Jiménez 3717* (F, MO); *Molina et al. 18018* (F, MO). Vic. of El General, *Skutch 2189* (GH, MO, NY, US), *3817* (F, GH, US), *3875* (GH, MO, NY, US), *3876* (GH, MO, NY, US). Cordillera de Talamanca, *Williams et al. 28449* (F, MO).

CUBA. LAS VILLAS: Trinidad Mts., *Gonzáles 469* (A, MO). ORIENTE: Rd. to El Caney, *Clemente 5690* (GH). Sierra de Nipe, *Ekman 10095* (F, NY, US), *10108* (NY, US). Papayo, *Ekman 10318* (US). Sierra Maestra, *Ekman 10324* (US). SANTIAGO: Cuabitas, *Hamilton 218*(NY). SANTA CLARA: Hoya de Manicaragua, *Britton et al. 4694* (NY). Trinidad Mts., *Brues s.n.* (GH, NY). San Blas, *Jack 6443* (US), *7053* (GH, NY). Banao Mts., *Luna 1004* (NY), *1007* (NY), *1008* (NY). Rincón to Banao, *Shafer 12323* (F, NY, US).

DOMINICAN REPUBLIC. BARAHONA: NW of Barahona, *Howard 12237* (GH, IJ, NY). LA VEGA: Jarabacoa, *Augusto 936* (NY). 12 km S of La Vega, *Davidse 2680* (MO). Constanza, *Jiménez 2123* (US). SAMANÁ: Vic. of Sánchez, *Abbott 181* (US). Vic. of Laguna, *Abbott 332* (US). SÁNCHEZ RAMÍREZ: Cotuy, *Abbott 737* (US). SAN JUAN: Piedra del Aguacate to Río del Oro, *Howard & Howard 9454* (GH, NY). SANTIAGO: Vic. of Santiago, *Allard 14557* (A, US). La Cumbre, *Jiménez 982* (US). SANTO DOMINGO: Vic. of Ciudad Trujillo, *Allard 13452* (NY, US), *13574* (US), *14157* (MO), *14457* (US), *14788* (US), *17941* (US). Llano Costero, *Ekman 11157* (A, US), *14219* (US).

ECUADOR. CHIMBORAZO: Near Huigra, *Camp 3039* (F, GH, NY, UC, US); *Hitchcock 20607* (US); *Rose & Rose 22184* (GH, NY, US). EL ORO: Between Santa Rosa and La Chorita, *Hitchcock 21146* (US). Between La Chorita and Portovelo, *Hitchcock 21196* (US). Near Santa Rosa, *Mexia 6725* (UC, US). Vic. of Portovelo, *Rose & Rose 22401* (US), *23374* (US). ESMERALDAS: Lita, *Jativa & Epling 889* (NY). Concepción and Guimbicito, *Solís 19720* (US). GUAYAS: 4 km W of Guyaquil, *Asplund 5802* (US), *5810* (US). Guayaquil, *Hitchcock 20133* (GH, NY, US), *20158* (US), *20236* (GH, NY, US). Milagro, *Hitchcock 20295* (GH, NY, US). Cerro de Isera, *Jativa & Epling s.n.* (NY). IMBABURA: Lita, *Solís 12142* (US). LOS RÍOS: Río Rita, *Asplund 5496* (NY). Río Palenque Biological Station, *Dodson 5821* (MO). 21 km S of San Carlos, *Gentry 9992* (MO). Vic. of Montalvo, *Holm-Nielsen et al. 2605* (AAU). Pichilingue, *Solís 10696* (F, US). Rd. from Napo to Puyo, *Ellenberg 3281* (MO). NAPO: Lago Agrio Airport, *Gentry 9835* (MO). PASTAZA: Vic. of Puyo, *Skutch 4392* (A, F, MO, NY, US). Arajuna, *Solís 9773* (US). SANTIAGO ZAMORO: Near Mendez, *Camp E-911* (NY, US). TUNGURAHUA: Between Baños and Cashurco, *Hitchcock 21775* (US), *21806* (US), *21808* (US). Río Mapato and Río Pastaza, *Penland & Summers 193* (F, GH). Near Baños, *Solís 10263* (F, US).

EL SALVADOR. SAN SALVADOR: Tonacatepeque, *Calderón 509* (GH, NY, US). Lomas de Candelaria, *Calderón 2514* (F, US). W side of Lake Ilopango, *Hitchcock 8921* (US). Vic. of San Salvador, *Standley 23117* (US).

FRENCH GUIANA. Saül, *Hoock 91* (CAY). Route de Kourou, *Hoock 325* (CAY, NY).

GUATEMALA. BAJA VERAPAZ: Sierra de las Minas, *Kellerman 6233* (US). IZABAL: Los Amates, *Deam 10* (F, GH, NY); *Kellerman 4786* (US), *7472* (US). Between Los Amates and Quiriguá, *Steyermark 38328* (F). PETÉN: Dolores, *Contreras 2283* (US). Between Río San Diego and San Diego, *Steyermark 45402* (F, US). RETALHULEU: Retalhuleu, *Bernoulli & Cario 885* (GOET), *953* (GOET). 5 km W of Retalhuleu, *Standley 87374* (F). Vic. of Retal, *Standley 88733* (F). ZACAPA: 13 km E of El Lobo, *Harmon & Fuentes 1857* (MO). Piedra Blanca de Gualán, *Pittier 1787* (US).

GUYANA. Rupununi, *Cook 173* (A, US). Kanuku Mts., *Smith 3314* (F, GH, MO, NY, US).

HAITI. L'ARTIBONITE: Vic. of Mission, *Leonard 3654* (NY), *3670* (IJ, NY, US), *3976* (NY, US). Vic. of Kalacroix, *Leonard 7910* (MO, US). Vic. of Ennery, *Leonard 9042* (NY, US). Marmelade, *Nash & Taylor 1252* (NY). NORD: La Victoria, *Holdrige 1738* (NY). St. Michael de l'Atalaye, *Leonard 7158* (GH, US), *7606* (US), *7776* (F, GH, NY, US), *8475* (US). Vic. of Plaisance, *Leonard 9282* (US), *9352* (US). Vic. of Pitala, *Leonard 9668* (IJ, US). NORD OUEST: St. Louis du Nord, *Leonard & Leonard 14197* (GH, NY, US). OUEST: Port-au-Prince, *Ekman H2224* (A, IJ, US). Vic. of Furcy, *Leonard 4563* (US).

HONDURAS. ATLANTIDA: 17 km SSE of La Ceiba, *Davidse & Pohl 2197* (ISC, MO). PARAÍSO: Danlí to Finca La Emilia, *Carlson 2568* (F). Vic. of Danlí, *Standley 16392* (F).

JAMAICA. CLARENDON: 1.25 mi WSW of Kellits Post Office, *Proctor 24633* (IJ). HANOVER: Lucea, *Hitchcock s.n.* (MO). MANCHESTER: New Forest, *Hitchcock 9837* (US), *9892* (US), *9893* (UC, US). Somerset Woods, *Proctor 16025* (IJ). Walderston, *Proctor 22915* (IJ). PORTLAND: Spring Hill, *Adams 9890* (M). Port Antonio, *Hitchcock s.n.* (MO, US); *Rothrock 420* (F, NY). ST. ANDREW: Silver Hill, *Davidse & Proctor 3247* (ISC, MO). Above Gordon Town, *Davidse & Proctor 3250* (ISC, MO). Mt. Lebanon, *Harris 12488* (F, GH, MO, NY, US). Gordon Town, *Hart 685* (NY, US); *Hitchcock 9380* (US), *9382* (US). Mt. Charles Dist., *Proctor 9626* (IJ, NY, US). St. Andrew, *Perkins 1138* (GH). Rd. to Bellevue, *Yuncker 17407* (F, MO). ST. ANN: Moneaque, *Adams 10022* (MO). ¾ mi NE of Faith's Pen Post Office, *Howard & Proctor 14990* (A, IJ). Mt. Diablo, *Ridley 24* (US). ST. CATHERINE: 4 mi S of Ewarton, *Adams 8946* (MO). Lluidas Vale, *Hunnewell 15227* (IJ). ST. JAMES: Flamstead, *Harris 11469* (F, GH, NY, US). Near Montego Bay, *Ridley 34* (US). ST. THOMAS: St. Thomas, *Britton 4045* (NY). Rd. to Landewey, *Davidse & Conroy 3257* (ISC, MO). 2.4 mi SE of Cedar Valley, *Davidse & Conroy 3266* (ISC, MO). Below Penlyne Castle, *Proctor 9588* (IJ). Above Bath Fountain, *Proctor 9792* (IJ). Between Easington and Llandewey, *Proctor 24239* (IJ). Vic. of Creighton's Hall, *Proctor 24243* (IJ). TRELAWNY: Troy, *Harris 12650* (F, GH, MO, NY, US); *Hitchcock 9808* (US), *9817* (US).

LEEWARD ISLANDS. ANTIGUA: Christian Valley, *Box 115* (US). Boggy Peak, *Rose et al. 3453* (NY, US), *3484* (NY, US). Fig Tree Hill, *Rose et al. 3493* (NY, US), *3647* (US). GUADELOUPE: *Duss 3182* (NY), *3183* (F, GH, MO, NY, US), *2683* (NY), *3613* (NY, US). Alymes, *Questel 4803* (P). Basse-Terre, *Sastre et al. 2539* (MO). Near St. Claude, *Stehlé 112* (US), *113* (US). Malanga, *Stehlé 1945* (GH, US). MONTSERRAT: Above Salem, *Proctor 18854* (A). Chancers Mtn., *Shafer 253* (F, NY, US), *255* (F, NY, US). Blakers, *Shafer 701* (F, NY, US). ST. KITTS: *Box 160* (NY); *Hitchcock 16353* (US).

MEXICO. CHIAPAS: 15 km SW of Suchiapa, *Breedlove 28079* (MO). Near Laguna Miramar, *Sohns 1604* (US), *1617* (US). OAXACA: Yaveo, *Mexia 9252* (MO). N of Tuxtepec, *Nelson 372* (US). VERACRUZ: Córdoba, *Bourgeau 1459* (P). Zacuapan, *Purpus 6206* (F, MO, NY, US).

NICARAGUA. CARAZO: Jinotepe, *Hitchcock 8674* (US), *8690* (GH, UC, US). CHONTALES: Near Santo Domingo, *Bunting & Licht s.n.* (F, NY); *Narvaez 3356* (MO). MATAGALPA: 6–10 km NE of Matagalpa, *Williams et al. 24032A* (F). 15 km NE of Matagalpa, *Williams et al. 27506* (F, MO, NY). ZELAYA: El Recreo, *Long 243* (F). Vic. of El Recreo, *Standley 19303* (F), *19518* (F). Vic. of Wani, *Stevens 7214* (MO).

PANAMA. BOCAS DEL TORO: Vic. of Chiriquí Lagoon, *von Wedel 1856* (GH, MO, US). CANAL ZONE: Summit, *Allen 2281* (MO, NY, US). Between Miraflores and Panamá, *Blum 2059* (MO). Colón–Empire, *Crawford 451* (NY). Barro Colorado Island, *Croat 4259* (MO, NY), *7474* (MO), *8009* (MO), *12942* (MO). Near Summit, *Croat 12791* (MO, US). N of Paraíso, *Croat 12974* (MO). Gamboa, *Croat 14603* (MO, US). Near Paraíso, *Dwyer 7150* (GH, MO, NY). Chagres, *Fendler 371* (MO). Balboa, *Greenman & Greenman 5052* (MO, US). Gatún Lake, *Hitchcock A.G.N.H.416* (MO), *A.G.N.H.417* (F, GH, MO, NY, US). Pedro Miguel, *Hitchcock 7955* (US). Gatún, *Hitchcock 9177* (UC). Las Cruces Tunnel, *Hunter & Allen 760* (GH, MO). Fort Kobbe, *Morton s.n.* (MO). Near Culebra, *Pittier*

2118 (NY). Between Corozal and Miraflores, *Pittier 2196* (NY). Summit, *Popenoe 26* (F, NY, US). Gatún Lake, *Popenoe 47* (F, NY). Barro Colorado, *Shattuck 528* (F, MO). Balboa, *Standley 25452* (GH). Near Culebra, *Standley 25955* (US). Balboa, *Standley 26065* (MO), *29319* (NY, US). Fort Clayton, *Tyson & Blum 3902* (MO). Near Miraflores Lake, *Tyson & Blum 4011* (MO); *White 56* (MO). CHIRIQUÍ: Burica Peninsula, *Croat 21968* (MO), *22020* (MO), *22050* (MO). Paso Canoas to Cañas Gordas, *Croat 22209* (MO). Burica Peninsula, *Croat 22513* (MO), *22553* (MO). 7 km W of Puerto Armuelles, *Croat 35016* (MO). 1 mi E of Cañas Gordas, *Liesner 267* (MO). 17 km NE of San Felix, *Nee 10759* (MO). COCLÉ: Río Mata, *Allen 142* (A, MO, US). 1.2 km N of El Cope, *Hammel 977* (MO). 178 km W of Panamá City, *Folsom 6890* (MO). 4 mi W of Antón, *Tyson & Blum 2598* (MO). COLÓN: Puerto Pilón, *Allen 4102* (F, NY). DARIÉN: Río Pinas, *Duke 10569* (MO). Isla Casaya, *Duke 10877* (MO). LOS SANTOS: 12 mi S of Macaracas, *Tyson et al. 3078* (MO). 16 mi S of Macaracas, *Tyson et al. 3096* (MO). PANAMÁ: 1 mi E of Tocumen Airport, *Blum & Tyson 1962* (MO). Santa Rita Ridge, *Correa 885* (MO). N of Buenos Aires, *Croat 12924* (MO, US). 3 km S of Alcalde, *Díaz 8857* (MO). Beginning of El Llano-Cartí Rd., *Dwyer & Nee 11994* (MO). Isla Bayano, *Garibaldi 81* (MO). Near Río Boquerón, *Hammel 894* (MO). San José Island, *Johnston 1078* (GH, US), *1272* (GH, US). El Llano-Cartí Rd., *Nee & Dwyer 9251* (MO). Matías Hernández Exp. Sta., *Pittier 6924* (GH, NY). Near Panamá, *Standley 26780* (GH), *29720* (US). Between Las Sabanas and Matías Hernández, *Standley 31837* (US). Between Matías Hernández and Juan Díaz, *Standley 32022* (US). Los Pozos–Chame, *Troetsch 22* (MO). SAN BLAS: Mulatuppa, *Duke 8530* (MO). VERAGUAS: Between Cañazas and the Cordillera Central, *Allen 176* (MO, US). 5 mi NW of Santa Fé, *Croat 23187* (MO). S of Santa Fé, *Nee 8054* (MO), *8106* (MO). 5 km S of Santa Fé, *Nee 8136* (MO). 2 km NW of Atalaya, *Nee 8201* (MO). 6–7 km N of Santa Fé, *Nee 9836* (MO). Cerro San Cristobal, *Nee 10158* (MO).

PARAGUAY. ALTO PARANÁ: Pte. Franco, *Bertoni 1413* (NY). Alto Paraná, *Fiebrig 6014* (GH, US), *6134* (GH, M). Nacunday, *Montes 10995* (US). BOQUERÓN: Gran Chaco, *Hassler 2868* (P). Puerto Casado, *Rojas 2722* (US). CAAGUAZÚ: Vic. of Caaguazú, *Hassler 9143* (GH, NY, P, UC). CETRAL: Yaguarón, *Arenas 1197* (MO). L'Assumption, *Balansa 40* (GOET, P). Cordillera de Altos, *Hassler 3731* (NY). Near Ypacaray, *Hassler 12514* (MO, NY, UC, US). Near Sapucay, *Hassler 13015* (US). Asunción, *Morong 641* (GH, MO, NY, US). Central Paraguay, *Morong 755* (GH, MO, NY, US). Near Asunción, *Morong 780* (NY). Villa Elisa, *Pedersen 5899* (A). Asunción, *Schinini 4728* (ISC, MO). CONCEPCIÓN: Between Río Apa and Río Aquidaban, *Fiebrig 4710* (GH). SAN PEDRO: Alto Paraguay, *Woolston G-87* (GH, NY, UC), *G-146* (NY, UC).

PERU. AMAZONAS: Río Cenepa, *Ancuash 452* (MO), *562* (MO), *677* (MO). Huampami, *Berlin 1966* (MO). Río Cenepa, *Kayap 744* (MO). Quebrada Satik, *Kayap 1096* (MO). Valley of Río Marañon, *Wurdack 1806* (US). AYACUCHO: Estrella, *Killip & Smith 22646* (F, GH, NY, US). Near Kimpitiriki, *Killip & Smith 22910* (NY, US). Estrella, *Killip & Smith 30674* (NY, US). CUZCO: Wajyumbe, *Vargas 720* (US). Quince Mill, *Vargas 9557* (US). HUÁNUCO: Pozuzo, *Macbride 4563* (F, US), *4571* (F, GH, US). Dist. Churubamb, *Mexia 8233* (F, GH, MO, NY, UC, US). JUNÍN: Near San Ramón, *Constance & Tovar 2240* (UC). Montayaco, *Gentry & Prance 16430* (MO). Colonia Perene, *Hitchcock 22118* (US), *22120* (US), *22122* (US), *22125* (US), *22502* (US), *22503* (US), *22504* (GH, US). La Merced, *Killip & Smith 23438* (F, NY, US). Río Pinedo, *Killip & Smith 23641* (NY, US). La Merced, *Killip & Smith 23998* (F, NY, US). Puerto Bermudez, *Killip & Smith 26441* (F, NY, US). La Merced, *Macbride 5298* (F, GH, NY, US). LORETO: Above Yurimaguas, *Croat 18083* (MO). Balsapuerto, *Killip & Smith 28673* (F, NY, US). Río Corrientes, *McDaniel & Marcos 11097* (MO), *11137* (MO). Near mouth of Río Nanay, *Rimachi 416* (MO). Pebas, *Williams 1782* (F, US). Lower Río Huallaga, *Williams 3918* (F, US), *4359* (F, US), *4939* (F, US), *5216* (F, US). MADRE DE DIOS: Puerto Maldonado, *Chávez 1807* (MO), *1810* (MO). Huancabamba, *Ferreyra 10793* (US). SAN MARTIN: Vic. of Tarapate, *Ferreyra 7876* (US). Juanjuí, *Klug 4372* (F, GH, MO, NY, UC). Tocache Nuevo, *Schunke 7467* (MO), *8241* (MO). San Roque, *Williams 7184* (F, US).

PUERTO RICO. Mt. Morales, *Britton & Cowell 443* (NY). Cuayara-Cayey Rd., *Britton et al. 6450* (NY). Vic. of Arecibo, *Chase 6457* (NY, US). Sierra de Luquillo, *Chase 6728* (US). Vic. of Mayagüez, *Chase 6809* (ISC, NY, US), *6822* (US), *6823* (US). Mariacao, *Duke 7362* (MO), *7580* (MO), *7607* (MO). 2 mi NE of Mayagüez, *Heller 4375* (F, GH, MO, NY, P). San German, *Hess 75* (US). Near Mayagüez, *Holm 74* (F, GH, MO, US), *116* (US). Río Piedras, *Otero 322* (MO). Luquillo, *Otero 510* (F, MO). Lares, *Sargent*

1381 (IJ). Mancao, *Sargent 13114* (US). Encata, *Shafer 2570* (NY, US). Coamo, *Sintensis 3062* (GH, GOET, P, US). Río Piedras, *Stevenson 2470* (F, NY). Yauro, *Velez 868* (NY).

SURINAM. Lely Mts., *Mori & Bolten 8486* (MO).

TOBAGO. Parlatuvier-Roxborough Trace, *Cowan 1481* (NY, UC, US). Speyside, *Hitchcock 10247* (US).

TRINIDAD. Caparo, *Broadway 4924* (US). St. Francique, *Broadway 4976* (RB, US). St. Ann's Cascade, *Broadway 5170* (A, F, ISC, MO). Rd. to Blue Basin Diego Martin, *Broadway 5873* (GH, MO). Aripo Rd., *Broadway 5991* (US). Maraval, *Broadway 7067* (F, MO, US). Maracas, *Broadway 7233* (MO). Moruga–La Fortune, *Broadway 7579* (US). Blanchisseuse Rd., *Broadway 7666* (MO). St. Anns, *Broadway 9164* (A, MO, US). Carcuage Main Rd., *Broadway 11286* (NY). Heights of St. Ann, *Britton et al. 665* (GH, NY). 1 mi W of Arima, *Davidse 2446* (ISC, MO). Northern Range, *Davidse 2460* (ISC, MO). 6 mi N of Port of Spain, *Davidse 2561* (ISC, MO). St. Anns, *Hitchcock A.G.N.H.594* (F, GH, MO, NY, US). Port of Spain, *Hitchcock 9950½* (US), *9963* (US), *9980* (US). Chacachacare, *Hitchcock 10061* (US), *10064* (US). Tabaquite, *Hitchcock 10131* (US). St. Joseph, *Hitchcock 10170* (US).

VENEZUELA. ARAGUA: El Castano, *Chase 12449* (US). Parque Nacional, *Chase 12454* (US, VEN), *12472* (GH, NY, US, VEN). Maracay, *Cornelia 78* (NY, US, VEN). Río Guayas, *Curran s.n.* (VEN). 19.8 km S of Carayaca, *Davidse 2902* (MO). Rancho Grande, *Davidse 3047* (MO). 7.4 km S of Alto de Choroní, *Davidse 3087* (MO). Ca. 5 km S of Alto de Choroní, *Davidse 3103* (MO). Colonia Tovar, *Fendler 1620* (GH, MO), *1631* (GH, MO). Vic. of Maracay, *Pittier 14968* (US, VEN). Parque Nacional, *Pittier 15278* (US, VEN). Between La Victora and El Consejo, *Williams 11026* (F, US). AMAZONAS: 12.5 km S of Puerto Ayacucho, *Davidse 2785* (ISC, MO, VEN). 20 km S of Puerto Ayacucho, *Davidse 2839* (ISC, MO, VEN). Ca. 5 km NNW of Sanariapo, *Davidse 2875* (ISC, MO, VEN). APURE: 42 km NW of Achaguas, *Davidse et al. 3923* (MO). BARINAS: Barinas, *Angelo 1077* (VEN). Near Barinitas, *Breteler 3417* (MO, NY, RB, US). 31 km NW of Mérida intersect., *Davidse 3184* (ISC, MO). 43 km NW of the Mérida intersect., *Davidse 3194* (ISC, MO). BOLÍVAR: La Gran Sabana, *Davidse et al. 4772A* (MO), *4782* (MO). El Pao Viejo, *Davidse et al. 4968* (MO). Between La Paragua and El Cristo, *Killip 37706* (US). Altiplanicie de Nuria, *Ramia 2260* (VEN). Salto Para, *Tillett 763-119* (MO). E of Miamo, *Steyermark 88188* (GH, NY, US, VEN). 22–25 km ESE of Santa Elena, *Steyermark et al. 112242* (MO). Headwaters of the Río Saca, *Wurdack & Guppy 99* (NY, VEN). CARABOBO: Near Bejuma, *Box 3940* (MO, VEN), *3943* (VEN). Maracay-Valencia, *Chase 12339* (US, VEN). Puerto Cabello, *Karsten s.n.* (GOET). DISTRITO FEDERAL: Sosa, *Badillo 18* (VEN), *38* (VEN). 19.8 km S of Carayaca, *Davidse 2902* (MO). GUÁRICO: 10 km S of San Juan de los Morros, *Davidse 3015* (MO). LARA: Aroa River, *Pittier 6384* (NY, US). MÉRIDA: Vic. of Tovar, *Pittier 12808* (VEN). MIRANDA: Los Teques, *Allart 211* (US). Sebastopal, *Badillo 115* (VEN). Entre Capaya y Curiepe, *Badillo 414* (VEN). Parque Nacional Guatopo, *Croat 21795* (MO). Cacarigua, *Curran 1* (VEN). Baruta–El Hatillo, *Gines 843* (VEN). Santa Lucia, *Killip & Tamayo 37030* (US, VEN). Silla de Caracas, *Morillo & Manara 1738* (MO, VEN). Valle de Siquire, *Pittier 5985* (NY, US, VEN). Vic. of Petare, *Pittier 9893* (GH, NY, US, VEN). Parque Nacional Guatopo, *Steyermark 90044* (NY, US, VEN). MONAGAS: Quiri Quiri to Caripito, *Chase 12580* (US, VEN). Cerro de la Cueva de Doña Anita, *Steyermark 88188* (GH, NY, US, VEN). PORTUGUESA: 20 km NE of Guanare, *Davidse 3149* (MO). SUCRE: Vic. of Cristóbal Colón, *Broadway 436* (GH, NY, US), *671* (US), *716* (GH, NY, US), *720* (GH, NY, US), *732* (GH, NY, US). Cerca Trapa, *Lasser & Lasser 3671* (VEN). TÁCHIRA: Between La Fria and Seboruco, *Breteler 4911* (VEN). TRUJILLO: Near Valera, *Pittier 10728* (GH, NY, US, VEN). YARACUY: Between San Felipe and Nirigua, *Aristeguieta & Panmier 1221* (VEN). Sierra de Aroa, *Aristeguieta & Panmier 1467* (VEN). Via Chivacoa, *Curran 53M* (VEN). San Felipe, *Curran 99* (VEN). Between Marin and Carbonero, *Pittier 11770* (NY, US, VEN). Entre Aroa y Altamira, *Steyermark & Bunting 105310* (MO). Guáguira, *Trujillo & Fernández 11* (MY). ZULIA: Cairo, *Lasser 2631* (VEN). Vegas del Río Santa Ana, *Pittier 10906* (GH, NY, US, VEN).

VIRGIN ISLANDS. ST. CROIX: Mt. Eagle, *Ricksecker 289* (F, MO, NY, US). Christiansted, *Rose et al. 3624* (US). ST. JOHN: *Morrow 17* (US). ST. THOMAS: Charlotte, *Millspaugh 520* (F, US). TORTOLA: Sage Mtn., *D'Arcy 537* (A), *538* (IJ). VIRGIN GORDA: *Fishlock 140* (US).

WINDWARD ISLANDS. BARBADOS: Welchman Hall Gully, *Proctor 25842* (IJ). Easy Hall Woods, *Proctor 26199* (IJ). DOMINICA: Sylvia Estate, *Cooper 26* (F, GH, NY, US), *26A* (NY, US). *Hitchcock 16415* (US). Morne Colla Anglais, *Hodge 1047* (GH, NY). South

Chiltern Estate, *Hodge & Hodge 1516* (GH). Providence Valley, *Hodge & Hodge 2069* (GH). Lisdara, *Hodge 2389* (GH, NY). Milton Estate, *Hodge & Hodge 2571* (GH), *2914* (GH). Castle Bruce, *Ramage s.n.* (GH). GRENADA: Richmond Hill, *Broadway 4674* (US). St. Georges, *Broadway s.n.* (NY). *Eggers 6224* (GOET, US); *Hitchcock 17675* (US). St. Patrick, *Proctor 17293* (A). MARTINIQUE: *Duss 770* (NY, US). St. Pierre, *Hahn 482* (P). *Hitchcock 16454* (US). Tiroli, *Stehlé 5436* (US), *5564* (US), *6028* (GH), *6150* (US). ST. LUCIA: Barre de l'Isle, *Cowan 1572* (A, NY, US). *Hitchcock 16494* (US); *Hunnewell 18975* (GH). Marigot Lagoon, *Smith 10199* (US). ST. VINCENT: St. George, *Proctor 25868* (IJ).

15b. **Lasiacis sorghoidea** (Devs.) Hitchc. & Chase var. **patentiflora** (Hitchc. & Chase) Davidse, Ann. Missouri Bot. Gard. 64: 375. 1978.

Lasiacis patentiflora Hitchc. & Chase, Contr. U.S. Natl. Herb. 18: 338. 1917. TYPE: Tobago, center of island, edge of woods on mountainside, 20 Dec. 1912, *Hitchcock 10268* (US-865566, holotype; US-975660, isotype).

Perennial; similar in most respects to *L. sorghoidea* var. *sorghoidea*, differs in the following respects; internodes glabrous; sheaths glabrous, the margin ciliate or glabrous, the auricular hairs 0.5–1.5 mm; collar usually puberulent, rarely glabrous; ligules 0.3–1.0(–1.7) mm long, ciliate with hairs to 1.0 mm; blades 6–18 cm long, 1.8–3.4(–4.5) cm wide, glabrous, sometimes slightly scabrous on the upper surface; panicles 4–22(–26) cm long, 2–10(–13) cm wide, the branches widely spreading, sometimes slightly reflexed, often rather open with flexuous, delicate pedicels, usually scabrous, the pulvini glabrous, occasionally puberulent; spikelets (2.8–)3.2–4.0(–4.2) mm long; first glume (1.3–)1.5–2.0 (–2.4) mm long; fertile floret 2.8–3.2 mm long, 1.7–1.9 mm wide, dark brown; caryopsis 1.7–1.8 mm long, 1.5–1.6 mm wide; chromosome number $n = 18$.

Ecology: This variety typically inhabits forest edges and brushy slopes at elevations from 200 to 2,000 m. Most specimens have been collected from November through February.

Distribution: This variety occurs in Venezuela, Colombia, Ecuador, and Paraguay in South America. In the West Indies, it is known from Hispaniola, Puerto Rico, and the following islands of the Lesser Antilles: Dominica, Grenada, and St. Vincent. In addition, it occurs on Tobago and Trinidad.

The plants from Tobago, Trinidad, and some from Venezuela are the most distinctive. They have glabrous leaves and spreading, open inflorescences with small spikelets borne on slender, delicate pedicels. Plants north and south of this center are closer to *L. sorghoidea* var. *sorghoidea*, differing only in their glabrous sheaths and blades, and the taxonomic distinction is correspondingly tenuous. The plants from these outlying areas have often been identified as *L. sloanei*. They resemble this species only in their glabrous leaves. The inflorescences never have the characteristic large, short-pedicelled, appressed spikelets of *L. sloanei*.

Localized in Venezuela are plants that have smaller leaves than is typical of *L. sorghoidea* var. *patentiflora*, and those plants closely resemble *L. divaricata* var. *austroamericana* and the glabrous small-spikelet form of *L. nigra*.

COLOMBIA. ANTIOQUIA: Vic. of Medellín, *Toro 377* (NY). CAQUETÁ: 15 km SW of Belen, *Davidse et al. 5692* (MO). HUILA: 32–33 km E of Neiva, *Fosberg 19777* (US). Inter Guadeloupe et La Resina, *Woronow & Juzepczuk 5744* (US). SANTANDER: Near Tapató,

Killip & Smith 20503 (GH, MO, NY, US). TOLIMA: Río Coello, *Killip 9732* (GH, NY, US). VALLE: La Cumbre, *Pennell 5402* (GH, US). VAUPÉS: San José de Guaviare, *Cuatrecasas 7464* (F, US).

DOMINICAN REPUBLIC. *Wright et al. 614* (US).

ECUADOR. GUAYAS: Teresita, *Hitchcock 20432* (US), *20524* (US). MORONA-SANTIAGO: Pachicutza, *Holm-Nielsen et al. 4543* (MO). PICHINCHA: 11 km W of Tandapi, *Gentry et al. 12110* (MO).

HAITI. NORD: Bayeux Morne Brigand, *Ekman 2624* (US). Massif du Nord, *Ekman 4330* (US). Vic. of Plaisance, *Leonard 9293* (US). SUD: Miragoâne, *Eyerdam 594* (F, GH, NY, US).

PARAGUAY. Pilcomayo River, *Rojas 292* (US).

PUERTO RICO. Vic. of San Juan, *Chase 6412* (US). Vic. of Mayagüez, *Chase 6824* (US).

TOBAGO. *Broadway 4841* (US). Pigeon Hill, *Cowan & Forster 1448* (NY, UC, US). Spey Side, *Hitchcock 10254* (US), *10255* (US), *10256* (US), *10257* (US). Center of island, *Hitchcock 10270* (US). Near Charlottesville, *Hunnewell 19912* (GH).

TRINIDAD. Port of Spain, *Hitchcock A.G.N.H.592* (F, GH, MO, NY, P, UC, US), *10034* (US), *10037* (ISC, US). Chacachacare, *Hitchcock 10062* (US). Port of Spain, *Hitchcock 10323* (US), *10324* (US). Manzanillo, *Hitchcock 10374* (US).

VENEZUELA. AMAZONAS: Río Negro, *Schultes & Lopéz s.n.* (US). ARAGUA: N of Maracay, *Box 3950* (VEN). 29 km S of Cua, *Steyermark 91783* (VEN). DISTRITO FEDERAL: Caracas Botanical Garden, *Berry 309* (MO). Between Caracas and La Guaira, *Fendler 1614* (MO). Caoma, *Jahn 303* (US, VEN). Near Naiguatá, *Steyermark 91813* (US, VEN). MÉRIDA: S of Mérida, *Chase 12385* (GH, NY, US, VEN). La Mucuy, *Lasser 540* (US, VEN). 2–4 km above Lagunillas, *Tillett & Hönig 738-337* (MO). MIRANDA: NE of Gran Felipe, *Aristeguieta & Panmier s.n.* (VEN). Near Sebastopal, *Badillo 113* (VEN), *313* (VEN). Parque Nacional Guatopo, *Steyermark 90036* (NY, US, VEN). Guarenas, *Williams 12402* (F, GH). MONAGAS: 14 km SW of Caripe, *Pursell et al. 9384* (NY, US). SW of Caripe, *Pursell et al. 9388* (NY, US). SUCRE: Vic. of San Cristóbal Colón, *Broadway 164* (GH, NY, US), *324* (GH, NY, US), *501* (GH, NY, US), *607* (GH, NY, US, VEN).

WINDWARD ISLANDS. BARBADOS: Turner Hale Wood, *Bovell & Freeman s.n.* (NY). DOMINICA: *Jones 49* (US). GRENADA: St. George, *Broadway 4446* (US). Richmond Hill, *Broadway 4674A* (P, RB, US). ST. VINCENT: Cannuoan Island, *Howard 11100* (GH). Bequia Island, *Howard 11276* (GH).

16. **Lasiacis standleyi** Hitchc., Proc. Biol. Soc. Wash. 40: 86. 1927. TYPE: Costa Rica, Guanacaste, La Tejona, north of Tilarán, moist forest, subscandent, 8 ft, 600–700 m, 25 Jan. 1926, *Standley & Valerio 45839* (US, holotype).

Lasiacis longiligula Swallen, Ann. Missouri Bot. Gard. 30: 232. 1943. TYPE: Panama, Canal Zone, forest along telephone cable trail between splice S16 and S49, Río Indio, trail toward Chico, 1 m tall, 12 Jan. 1935, *Steyermark & Allen 17435* (US, holotype; GH, UC, isotypes).

L. lucida Swallen, Ann. Missouri Bot. Gard. 30: 231. 1943. TYPE: Panama, Chiriquí, Volcán de Chiriquí, forest above Sabana de El Salto, on trail to Camp Aguacatal, 1500–1750 m, 10–13 Mar. 1911, *Maxon 5266* (US-675603, holotype; US-675607, US-186873, isotypes).

Perennial; culms creeping, rooting at the nodes, forming colonies, the distal ends erect to 1 m, or scrambling through shrubs up to several meters high; internodes 2–4 mm thick, herbaceous, hollow, often with striplike pith remains, puberulent toward the apex and with a line of puberulence, rarely pubescent with hairs to 1.5 mm long; nodes glabrous; sheaths puberulent, pubescent, or hispid with hairs to 3.0 mm long, occasionally glabrous, the upper margin sparsely to densely ciliate with hairs to 2.5 mm long, rarely both margins ciliate; collar glabrous or with a definite line of puberulence at its base; ligule a prominent, usually dark brown, lacerate membrane, (4.5–)5.0–7.0(–9.0) mm long, ciliate on at least one margin with hairs to 3.0 mm long, typically glabrous on the back; blades 10–18 cm long, (0.8–)1.2–2.9(–3.5) cm wide, broadly elliptic-lanceolate to linear-lanceolate, the upper surface usually strongly scabrous,

puberulent, or hispidulous, sometimes glabrous, the lower surface usually puberulent or hispidulous, sometimes glabrous, the apex acuminate, the base asymmetrical, the margins scabrid and often tending to be undulate; panicles rather compact, 7–27 cm long, the longest branch 2–15 cm, the branches usually ascending, occasionally widely spreading, producing secondary branches from near their bases and bearing spikelets almost throughout their length, or sometimes naked for ⅓ their length, scabrous, sometimes sparsely pubescent, the pulvini puberulent, the pedicels usually pubescent, occasionally scabrid; spikelets 3.7–4.5(–5.0) mm long; first glume 9–11-nerved; second glume 9–13-nerved, sterile floret without a flower, the lemma 11–13-nerved, the palea ⅓–¼ as long as the fertile floret; fertile floret 3.4–4.1 mm long, 2.2–2.5 mm wide, the anthers white, the stigmas purple; caryopsis 2.1–2.4 mm long, 1.7–2.0 mm wide; chromosome number $n = 18$.

Ecology: *Lasiacis standleyi* typically inhabits cloud or montane forests from 600 to 2,000 m. Although it does occur in undisturbed forest, it may be more frequent in clearings, along trails, and in thickets along road embankments in forested mountains. However, it is not a pioneer species and is more abundant in relatively stable secondary communities. It is rather uncommon. Flowering specimens have been collected from October to early April, although the majority of the collections have been made from December through March.

Distribution: *Lasiacis standleyi* is known in Central America from Chiapas to Panama, excluding El Salvador, and in South America from Colombia, Venezuela, and Ecuador.

This creeping species is distinguished by its hollow culms, moderately broad, short leaves, very long ligule, and rather compact inflorescences whose spikelets have short sterile paleas and no staminate flowers. It is effectively separated from all other creeping species except *L. grisebachii* by its hollow culms. From the latter species, it can be distinguished by its broad leaves and long ligules. *Lasiacis standleyi*, aside from its hollow culms, resembles *L. rhizophora* most closely. From this species, it can best be separated by its long ligules and the evenly distributed spikelets. Spikelets of *L. rhizophora*, on the other hand, are arranged in clusters toward the ends of the panicle branches. Hitchcock (1927a) mistakenly stated that *L. standleyi* and *L. rhizophora* have similar inflorescences.

Most of the South American specimens that I have identified as *L. standleyi* have previously been identified as other species. Many of these have been named *L. oaxacensis*. This species has solid culms, however. Other common misidentifications have been *L. ligulata* and *L. scabrior*, both erect woody species. *Lasiacis ligulata* can be easily distinguished from *L. standleyi* by its shorter ligule. *Lasiacis scabrior* is similar to *L. standleyi* in having large, prominent ligules, but it differs most prominently in its small panicles which are partially included in the upper sheath.

Few of the available South American specimens adequately show the basal parts of the plants. The culms of these plants may often become very vigorous and grow into large tangles. They, therefore, rarely show roots at the upper nodes. Unfortunately, only the upper parts of the plant are usually collected.

These specimens can often be recognized by their relatively wide, rather herbaceous, often collapsed culms, as well as by the other characters previously enumerated.

Lasiacis standleyi is a variable species, some forms of which have been named as separate species, *L. lucida* and *L. longiligula*, by Swallen (1943).

Lasiacis lucida was distinguished by Swallen (1943) from *L. standleyi* and *L. longiligula* primarily by its larger spikelets (5 mm vs. 4 mm). This single distinguishing character is quite inadequate. Only the type of *L. lucida* and one other collection (*Stern, Eyde & Ayensu 2032*) have such large spikelets. There are a number of specimens with intermediate spikelet sizes, but the majority are 3.8–4.2 mm long.

Lasiacis longiligula was distinguished from *L. standleyi* primarily on the basis of a larger ligule and panicle branches bearing spikelets in clusters at the ends of the branchlets (Swallen, 1943). The panicle branches of the holotype of *L. longiligula* are naked only two-sevenths their length or less, rather than one-third to one-half attributed to it in the description by Swallen. The whole panicle is rather densely flowered. Looser, less densely compact inflorescences do occur in this taxon. But there is no clear line of demarcation between the two types of panicles. The larger inflorescences nearly always have the lower parts of the inflorescence branches naked, but this is probably correlated with the amount of branching and vigor of the plant rather than distinct genetic differences. No discontinuities exist in ligule size, numerous specimens having ligule sizes ranging from 5–8 mm.

Abnormally long, pointed spikelets, somewhat reminiscent of some *Ichnanthus* spikelets, occur in *Skutch 4460* from Ecuador. These are mixed with normal spikelets (6.5 mm vs. 4.0 mm in length) on the F specimen. In each long spikelet there is a single insect larva, which presumably through hormonal stimulation causes the abnormal spikelet growth.

COLOMBIA. CALDAS: Río Santa Rita, *Killip & Hazen 10138* (US). CAUCA: Micay Valley, *Killip 7714* (GH, NY, US). Río Hondo, *Killip 8259* (GH, NY, US). Above Palmira, *Pittier 875* (US). PUTUMAYO: Below Sachamates, *Fosberg 20370* (US). VALLE: Hoya del Río Sanjuniquia, *Cuatrecasas 15602* (F, US). Palmira, *Killip 6149* (NY, US). El Silencio, *Killip & Garcia 33774* (COL, US).

COSTA RICA. ALAJUELA: San Ramón, *Brenes 13460* (F, NY), *20319* (NY). 3.5 km SE of Tapantí, *Lent 790* (F). Between La Hondura and La Palma, *Pohl & Davidse 11210* (ISC). Villa Quesada, *Smith P2512* (F, MO). CARTAGO: Vic. of Pejivalle, *Skutch 4571* (F, GH, MO, NY, US), *4649* (F, GH, MO, NY, US); *Standley & Valerio 47160* (US). El Muñeco, *Standley & Torres 50979* (US). GUANACASTE: Tilarán, *Acosta 9* (F). Volcán Rincón de la Vieja, *Pohl & Davidse 11675* (ISC, MO); *Pohl & Erickson 12665* (ISC). La Tejona, *Standley & Valerio 45820* (US). Near Tilarán, *Standley & Valerio 45532* (US). Quebrada Serena, *Standley & Valerio 46140* (US). Tilarán, *Valerio 1156* (F). Volcán Orosí, *Wilbur & Stone 10214* (MO). HEREDIA: Vara Blanca, *Skutch 3674* (MO, NY, US), *3680* (GH, MO, NY, US). Yerba Buena, *Standley & Valerio 50068* (US). PUNTARENAS: 1 mi SW of Cañas Gordas, *Croat 22279* (MO). Osa Peninsula, *Godfrey 66916* (NY, US). 4 km S of San Vito de Java, *Raven 20891* (F). Vic. of Buenos Aires, *Tonduz 3646* (US), *6540* (US). SAN JOSÉ: Vic. of El General, *Skutch 2206* (GH, MO, NY, US). Vara Blanca, *Skutch 3674* (US), *3680* (US). Vic. of El General, *Skutch 3802* (GH, MO, NY, US).

ECUADOR. NAPO: Vic. of Puyo, *Skutch 4460* (A, F, MO, NY, US). TUNGURAHUA: Valley of the Pastaza River, *Hitchcock 21894* (GH, NY, US).

GUATEMALA. SUCHITEPÉQUEZ: Finca Mocá, *Hunnewell 14627* (GH).

HONDURAS. ATLANTIDA: 3 km S of Lancetilla, *Molina 10467* (US). CORTES: N of Lake Yojoa, *Morton 7619* (NY). MORAZÁN: Vic. of El Zamorano, *Freytag 222* (MO), *306* (WIS).

MEXICO. CHIAPAS: 13 km N of Berriozábal, *Breedlove 31256* (DS, MO). Laguna Ocotal Grande, *Breedlove 32999* (DS, MO).

NICARAGUA. MATAGALPA: N of Santa Maria de Ostuma, *Williams et al. 24919* (F, NY), *27750* (F).

PANAMA. CANAL ZONE: Trail toward Chico, *Steyermark & Allen 17435* (UC). CHIRIQUÍ: Vic. of New Switzerland, *Allen 1338* (F, GH, MO, NY). 2.5 km N of Bambito, *Cochrane et al. 6296* (MO). 3 mi N of Volcán, *Croat 13559* (ISC). 1 mi E of Cañas Gordas, *Croat 22331* (ISC, MO). Above San Felix, *Croat 33047* (MO). Cerro Colorado, *Folsom et al. 4845* (MO). La Fortuna, *Hammel 2269* (MO). Volcán Chiriquí, *Hitchcock 8199* (in part) (UC, US). 2 mi above Boquete, *Killip 1529* (US). Vic. of Boquete, *Stern et al. 2032* (US). DARIÉN: Cerro Mali, *Gentry & Mori 13855* (MO). Cerro Tacarcuna, *Gentry & Mori 14090* (MO). Cerro Sapo, *Hammel 1134* (MO), *1310* (MO). HERRERA: Above Chepo de las Minas, *Folsom et al. 6996* (MO), *6970* (MO). LOS SANTOS: 25 mi SW of Tonosí, *Lewis et al. 2896* (COL, MO). PANAMÁ: Cerro Azul, *Croat 17298* (MO). Cerro Campana, *Croat 22784* (MO); *Dressler 3942* (MO). Cerro Azul, *Duke 9345* (MO). Cerro Campana, *Dwyer et al. 4728* (MO). Cerro Jefe, *Dwyer et al. 7239* (MO); *Dwyer & Gentry 9498* (MO); *Gentry et al. 3515* (MO). Cerro Campana, *Lewis et al. 3048* (COL, MO, UC). 3 mi NE of Altos de Pacora, *Liesner 527* (MO). Cerro Azul, *Nee 9295* (MO); *Porter et al. 4094* (MO). Cerro Campana, *Porter et al. 4272* (MO), *4882* (MO). La Eneida, *Soderstrom 2007* (ISC, MO). Cerro Campana, *Wilbur & Weaver 11300* (MO). VERAGUAS: NW of Santa Fé, *Mori & Kallunki 5315* (MO).

VENEZUELA. TRUJILLO: Entre Escuque and La Mesa de San Pedro, *Steyermark 104658* (VEN). ZULIA: Sierra de Perijá, *Steyermark et al. 105551* (MO). Río Apón, *Vareschi 3166* (VEN).

17. Excluded Species and Names of Uncertain Status

Lasiacis excavata (Henrard) Parodi, Notas Mus. La Plata, Bot. 8: 92. 1943.

Panicum excavatum Henrard, Repert, Spec. Nov. Regni Veg. 23: 179. 1926. TYPE: Paraguay, Guarapi, dans les forets, tiges radicantes, 1881, *Balansa 2947* (L, holotype).

Parodi (1943) transferred this species to *Lasiacis* on the basis of the small cratiform depression at the apex of the fertile lemma in which is borne a fine pubescence. There are no other spikelet characters in common with *Lasiacis*. The very narrow spikelets borne erect on the pedicels are quite different from anything found in *Lasiacis*. For this reason, I exclude this species from *Lasiacis*. As Parodi (1943) noted, the base of the fertile lemma does have a depression reminiscent of those in *Ichananthus*. The real affinity may lie with this genus or with the *Panicum* species closely related to *Ichnanthus*.

Panicum divaricatum L. var. *latifolium* Fourn., Mex. Pl. 2: 33. 1886, non *P. divaricatum* var. *latifolium* Schlecht. & Cham., 1831.

The ten specimens cited by Fournier under this variety represent a mixture of *L. ruscifolia* and *L. nigra*.

Panicum maculatum Aubl., Pl. Guian. 1. 51. 1775. *Lasiacis maculata* (Aubl.) Urb., Symb. Ant. 8: 751. 1921.

The application of this epithet is uncertain. The species cannot be identified from the description. Urban (1919) used the name in place of *L. sorghoidea* (Desv.) Hitchc. & Chase. He based this on an unpublished (Hitchcock, 1927b) drawing of Plumier which was cited as a synonym of *P. maculatum* by Aublet (1775). Urban noted that "Aus der Abbildung Plumiers kann man nicht ersehen, ob *Lasiacis sorghoidea* (Desv.) Hitchc. et Chase oder die sehr nahe verwandte *L. sloanei* (Griseb.) Hitchc. vorliegt." He further stated that Plumier probably

described a plant from Martinique, and since *L. sloanei* did not occur there, the name must apply to *L. sorghoidea*. However, Aublet's description almost certainly was based on a plant from the Guianas. Since *L. ligulata* is the most common species in this region, the name may actually refer to *L. ligulata*. Stafleu (1967) indicated that the main fragments of Aublet's herbarium are at BM and P. It has not been possible to locate a type yet in these two herbaria. Until this can be done, it seems wise to follow Hitchcock (1920) is assigning this name to doubtful status.

Panicum ruscifolium H. B. K. var. *amblyoides* Fourn., Mex. Pl. 34. 1886.

No specimens are cited but five specimens are cited under the two subvarieties of this variety.

Panicum ruscifolium H. B. K. var. *amblyoides* Fourn. subvar. *glabra* Fourn., Mex. Pl. 34. 1886, nom. nud.

Panicum ruscifolium H. B. K. var. *amblyoides* Fourn. subvar. *pilosa* Fourn. Mex. Pl. 34. 1886, nom. nud.

Panicum scariosum Trin. ex Steud., Nom. Bot., ed. 2. 2: 263. 1841. nom. nud.

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A NEW *MATELEA* (ASCLEPIADACEAE) FROM THE BAHAMAS

David L. Spellman[1]

Preparation of a new account of the flora of the Bahamas by Dr. Donovan S. Correll of Fairchild Tropical Garden has led to recent intensive collections from those islands by Dr. Correll. The new taxon described below represents the first record of this large and interesting genus from these islands. While known from a number of other Caribbean islands, *Matelea* is nowhere as abundant nor diverse as in the tropical areas of the mainland land mass of North and South America.

Matelea correllii Spellman, sp. nov.—Fig. 1.

Caules scandens; foliis anguste ovatis, basibus rotundato-truncatis, inflorescentia fere epedunculata, corollis rotatis, viridibus, macula albo ad apicem, gynostegio rubrifusco, apice tholiformi, corona quinquiangulari, basaliter striata autem columna laevi, folliculo anguste obovoideo, quinqueali.

Slender *vines*; stems weakly and sparsely retrorse hispid when young, becoming glabrous. *Leaves* narrowly ovate, apically acute, mucronulate, basally truncate to slightly rounded, glabrous above and below except for short hairs along the margins and along the larger veins beneath, the lower surface somewhat pustulate at least when dry; blades mostly 5–7 cm long, 1.5–2 cm broad; petioles retrorse hispid, 0.5–0.7 cm long, a cluster of dactyliform glands at the juncture of petiole and blade. *Inflorescence* an interaxillary contracted umbelliform raceme, apparently 3–5 flowered, glabrous or nearly so; peduncles mostly ca. 2 mm long; pedicels 4–5 mm long. *Flowers* 13–15 mm in diameter; calyx deeply cut, glabrous on both surfaces, the lobes ovate, 3–3.5 mm long, mostly 2.5 mm wide, a single gland within the base of each sinus; corolla rotate, green with darker green venation, usually with a small white spot at the apex of each lobe, glabrous throughout, the tube ca. 1 mm long or less, the limb deeply cut, the lobes broadly ovate, 5.5–6.5 mm long, 4.5–5.5 mm wide; gynostegium ca. 1.5–2 mm high, red brown, the head sharply pentagonal, ca. 2.5 mm in diameter, terminated by a rounded dome with a shallow depression in its center; corona carnose, red brown, broadly pentagonal, 3 mm in diameter, appearing to consist of two distinct parts, a basal thickened striate portion rather sharply delineated from the upper skirt-like smooth portion which is slightly concave beneath each of the 5 anthers; pollinia compressed, broadly obpyriform, excavated on one side, 0.8 mm long, 0.4 mm wide, the corpusculum subsagittate, ca. 0.3 mm long, 0.2 mm wide, the translators ca. 0.7 mm long. *Follicles* narrowly obovoid, longitudinally 5-winged, puberulous when young, glabrous or nearly so at maturity, 7 cm long, 1.5–2 cm in diameter, the wings 1–2 cm wide; seeds flattened, ovate, ca. 5 mm long, 3.5 mm wide, the marginal wing ca. 0.5 mm wide, irregularly and vaguely serrate

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Ann. Missouri Bot. Gard. 65: 1255–1257. 1978.

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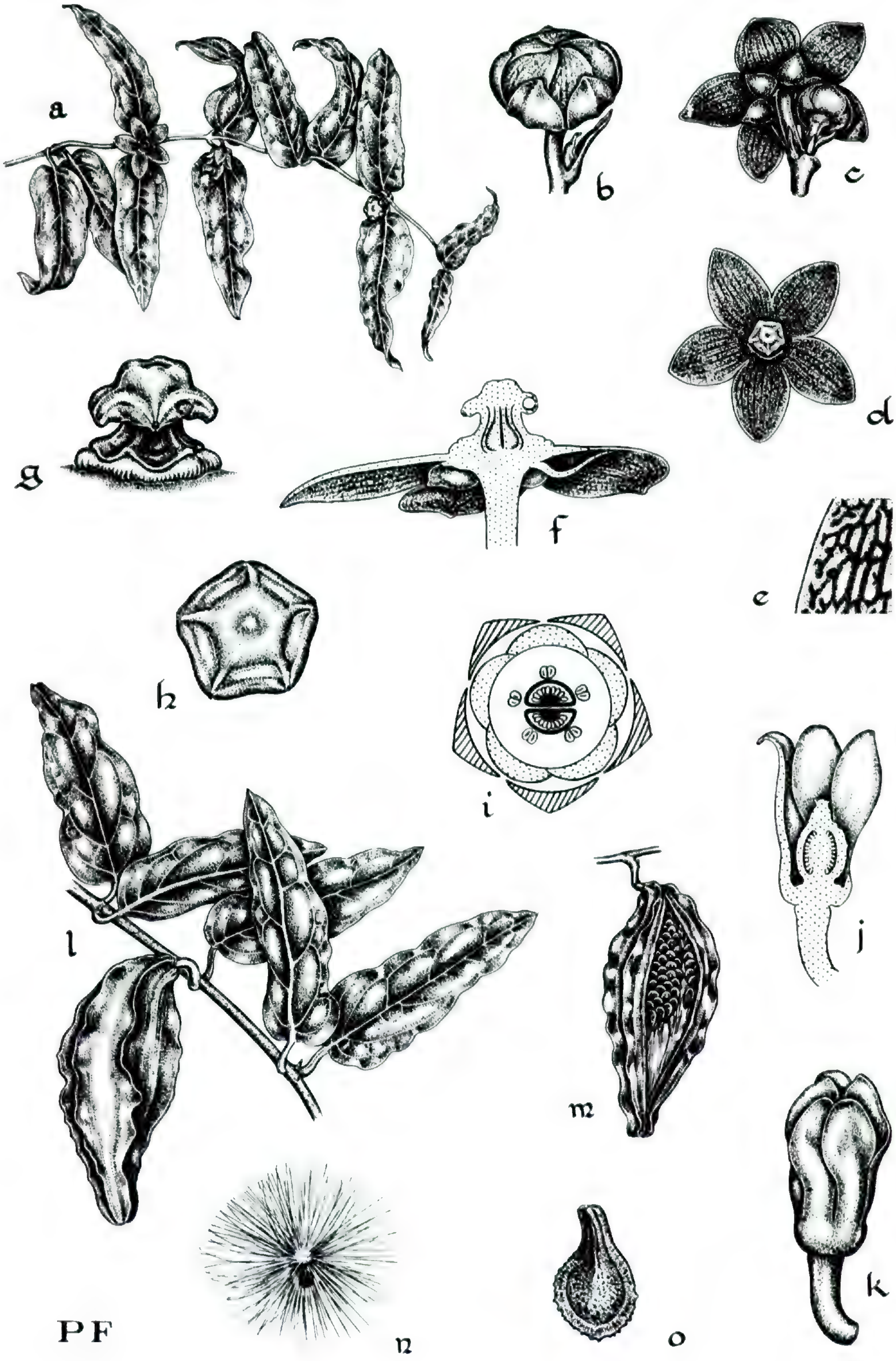
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at one end, surface minutely pustulate with dark broken reticulations scattered irregularly over the surface, the coma white, 2–3 cm long.

TYPE: BAHAMA ISLANDS. LONG ISLAND: Vine climbing on trees and shrubs in low places along Queen's Highway about 4 miles north of Clarence Town center, 18 Nov. 1977, *D.S. Correll 49112* (MO, holotype; F, FTG, GH, NY, US, isotypes).

Additional collection examined (fruiting): BAHAMA ISLANDS. LONG ISLAND: About 3 miles west of Clarence Town along Queen's Highway, on edge of low swampy area on north side of highway, vine on shrubs, 14 March 1977, *D.S. Correll 48157* (F, FTG, GH, MO, NY, US).

Except for its generally larger size, this species is remarkably similar to the Guatemalan-Belizean *M. pusilliflora* L. Wms. This resemblance is manifest in the glabrous usually truncate leaves, nearly sessile inflorescence, and dark green flowers with their white-tipped lobes. It also bears a superficial resemblance to *M. grisebachiana* Alain from Cuba, a species which is much more pubescent throughout, and has a larger corona which is more circular than angular.

←

FIGURE 1. ***Matelea correllii*** Spellman—a. Flowering stem (×½).—b. Flower bud (×3).—c. Inflorescence (×1½).—d. Flower (×1½).—e. Detail of corolla lobe venation (×6).—f. Flower, longitudinal section (×3).—g. Gynostegium (×6).—h. Gynostegium from above (×6).—i. Floral diagram.—j. Young fruit, longitudinal section (×3).—k. Corolla enfolded over young fruit (×3).—l. Fruiting stem (×½).—m. Dehiscing fruit (×½).—n. Seed with coma (×½).—o. Seed, coma removed (×3). Illustrated by Priscilla Fawcett.

THE BOTANY AND NATURAL HISTORY OF PANAMA

A symposium to signal completion of the Flora of Panama will be held in Panama 1–4 April 1980. Sessions will include the physical setting, archaeology, vegetation, flora, fauna and demography of Panama and nearby countries as well as other natural history related topics. Conservation of endangered landscapes will be a theme. Both invited and contributed papers will be given, and either Spanish or English may be used. Limited funds may be available to assist costs of attending this meeting. The symposium is sponsored jointly by the Missouri Botanical Garden, the University of Panama, and the Smithsonian Tropical Research Institute.

Contact: Prof. Mireya D. Correa A.
Escuela de Ciencias Naturales y Farmácia
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Republic of Panama

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The 1978 Jesse M. Greenman Award was presented to E. Hennipman, Rijksherbarium, Leiden, for the publication "A monograph of the fern genus *Bolbitis* (Lomariopsidaceae)."

F. Almeda, Jr. won the 1979 Award for his "Systematics of the genus *Monochaetum* (Melastomataceae) in Mexico and Central America.

The award of $250.00 is presented each year by the Alumni Association of the Missouri Botanical Garden. It recognizes the best paper in vascular plant or bryophyte systematics based on a doctoral dissertation published during the previous year. Papers published in 1979 are now being considered for the 13th Annual Award, to be presented in 1980. Reprints of such papers should be sent to Greenman Award Committee, Department of Botany, Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166 U.S.A. In order to be considered for the Award, reprints must be received by 1 July 1980.

ERRATA

The following typographical errors appeared in Vol. 65, no. 2:

P. 615, line 1, read 1816 for 1886
P. 778, line 25, read lewisii for lewissi

The previous issue of the ANNALS OF THE MISSOURI BOTANICAL GARDEN, Vol. 65, No. 3, pp. 782–998, was published on 20 March 1979.

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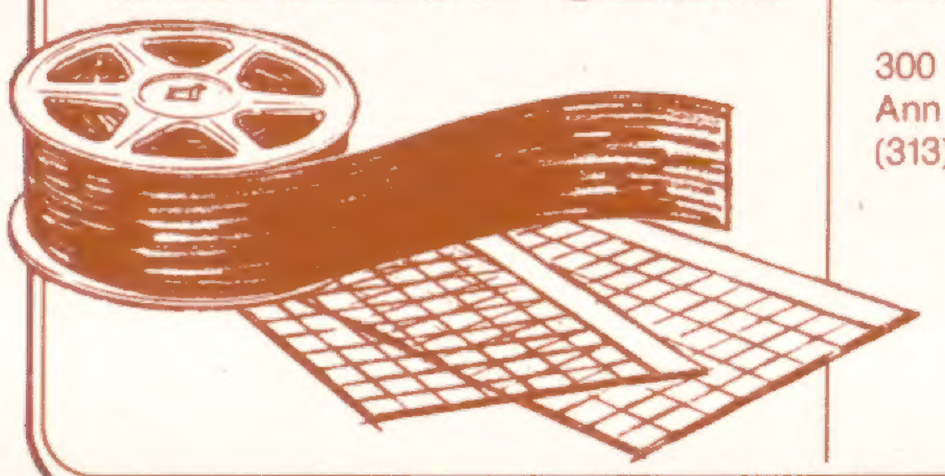

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